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The Oases of Central Baja California, México. Part I. A Preliminary Account of the Relict Mesophilic Herpetofauna and the Status of the Oases

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Abstract.—A preliminary account of the relict mesophilic herpetofauna of the oases of central Baja California supports previous hypotheses of an historical ecological transformation of central Baja California from a mesic to a xeric region. The general herpetological pattern that emerges is that a treefrog (*Hyla cadaverina* and/or *H. regilla*), a slider turtle (*Trachemys scripta*), and the two-striped garter snake (*Thamnophis hammondi*) usually occur in a particular oasis. Occasionally, other mesophilic lizards and snakes are found, as well. The hypothesis we present is that these mesophilic taxa had a continuous transpeninsular distribution during earlier wetter periods, but with the rapid desertification of central Baja California in the last 8000–10,000 years, these species have become restricted to the mesic refugia of oases in the central peninsular portion of their ranges. Unfortunately, many of the oases are being severely altered by direct and indirect human activities which, in some cases, have persisted for nearly 300 years since the Mission Period. Physical alterations include damming for irrigation, pumping for drinking water, and trampling by cattle. Biological alteration includes the introduction of non-native species of plants and animals. Such alterations have led to the extinction and/or decline of some of the mesophilic herpetofauna in some of the oases.

The Baja California peninsula is the second longest and most geographically isolated peninsula in the world. It has undergone a unique, complex tectonic origin (Gastil and Jensky 1973), which has resulted in its current physiography of sharp mountain ranges, large basins, and volcanic badlands. Concomitant with the geomorphological evolution of the peninsula was a radical ecological transformation of its central region, from an area of mesic subtropical forests and wooded grassland to one of xeric desert scrub (Axelrod 1979). Such a transformation has created many disjunct mesic refugia which remain primarily on mountain tops and in oases. The higher elevations of mountain tops harbor less xeric-adapted mesophilic taxa because temperatures are cooler and precipitation is greater than in the surrounding low-lying deserts. Oases support similar taxa because mesic habitats are found along the water's edge or in the water itself. Amphibians and reptiles restricted to such habitat "islands" are widely distributed throughout non-desert regions of cismontane and montane northern Baja California and California and/or the humid subtropical, tropical, and montane areas of the Cape Region.

This paper will be the first of a series focusing on the biology and conservation of the oases in central Baja California. Discussed here is the relict mesophilic

herpetofauna associated with the oases and the history of human utilization and alteration of these water systems. A population is considered to be a mesophilic relict if the species is not found in surrounding desert regions but is widespread outside such regions in nondesert areas. This includes terrestrial species common to chaparral communities of northern Baja California and California, species common to the more tropical and montane forests of the Cape Region, and semiaquatic and aquatic species of riparian habitats.

Materials and Methods

Thirty-one oases were visited in the course of this study. Oases are considered here to be isolated permanent or semipermanent bodies of spring-fed water along with their associated floras that occur south of the Sierra San Pedro Mártir and north of the Isthmus of La Paz. This definition excludes the well-watered streams and canyons along the eastern desert slopes of the northern Peninsular Ranges, including the Sierra San Pedro Mártir and Sierra Juárez. We do not believe that the mesophilic herpetofauna of these areas are truly isolated from the continuously distributed, wide-ranging cismontane and montane populations of their conspecifics. These desert foothill canyons are easily accessed by species simply dispersing along the streambed corridors down from the mountains. Thus, these water systems are not truly isolated nor is their mesophilic herpetofauna relict. Similarly, the well-watered areas of the more tropical Cape Region were not included. The oases considered here are surrounded by extensive expanses of desert and it would be highly unlikely that mesophilic amphibians and reptiles could, or would, disperse across such arid expanses to colonize these areas.

The oases were visited between June 1986 and July 1991, principally during the summer months. At each oasis, an attempt was made to observe the associated mesophilic herpetofauna. The majority of the observations were made first hand and documentary photographs were taken. Observations also were augmented by herpetofaunal descriptions from local ranchers. In such cases the line of questioning used to obtain this information was constructed in such a way as not to be leading or to bias their response.

Referenced phytogeographic regions (Fig. 1) follow the descriptions and characterizations of Grismer (1993). Museum abbreviations follow Leviton et al. (1980). Several references are made below alluding to introduced species of fishes in some of the water systems. Although we cannot identify these species, we have reason to believe that some of them are new and this will constitute a subsequent report in this series.

The historical documentation of water use and oasis alteration during the Mission Period was taken from the works of Clavijero (1789), Aschmann (1959), Mathes (1977), and Robertson (1990). The results of the impact of missionary use on the current water systems was evaluated.

Results

The 31 oases visited in the course of this study are different enough in location, adjacent phytogeography, size, and floral and faunal content that each requires its own characterization. The cases are discussed below from north to south.

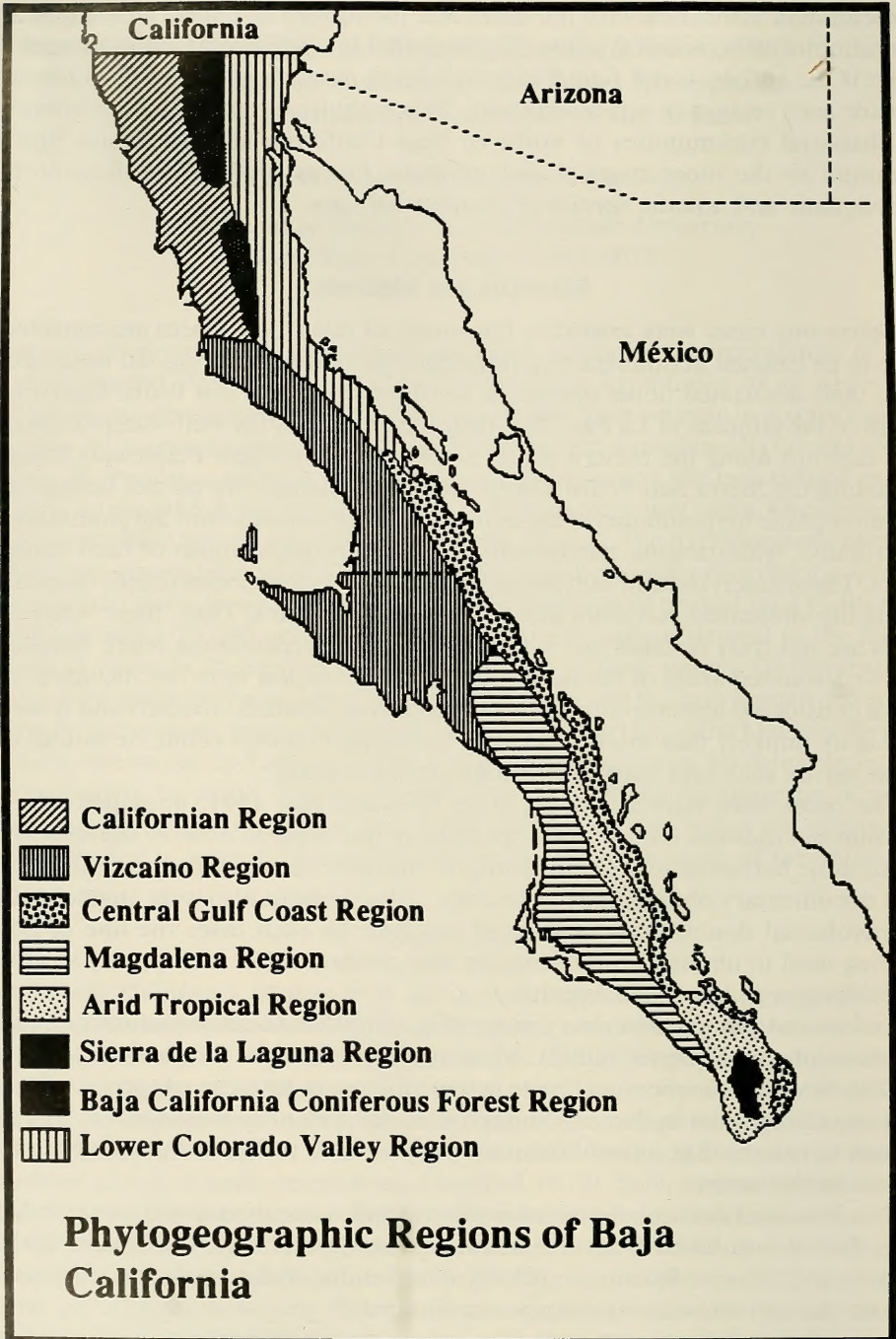


Fig. 1. Phylogeographic regions of Baja California following Grismer (1993) modified from Wiggins (1980).



Fig. 2. Location of the oases in Baja California. See Table 1 for an explanation of the La Presa Region.

Misión San Fernando Velicatá

Misión San Fernando [Rey de España de] Velicatá is located approximately 51 km east-southeast of El Rosario in Arroyo San Fernando [=Arroyo de Velicatá] (Fig. 2) within the Vizcaíno Region. The site of the mission in Arroyo San Fernando lies at the foot of a large rocky north-facing slope in a relatively broad valley with dense stands of acacias (Fig. 3). Here, the water is above ground year round and courses slowly past the mission site toward the west. The dominant stream side vegetation is *Salix* sp., *Juncus acutus*, and *Baccharis glutinosa*. This well-watered site was first discovered in 1766 by the Jesuits and was established as a military base camp for the Franciscan advance into Alta California in 1768. In 1769, the site was founded as the first Franciscan mission and persisted until 1808. During this time period, many rock canals and at least two dams were constructed for irrigation purposes by Cochimí Indian slaves under Franciscan dominance. These dams and canals are currently in use by two small ranchos on the original mission site. According to the inhabitants of these ranchos, these are the only areas where water has persisted through the annual dry season of the last five or six years. The Pacific treefrog (*Hyla regilla*), the California treefrog (*H. cadaverina*), and the two-striped garter snake (*Thamnophis hammondi*) have been found in the pools associated with the dams and in the canals (McGuire 1989). Local ranchers told us that turtles formerly occurred in the large ponds behind the dams. However, a large storm (*chubasco*) in 1978 resulted in heavy siltation of the ponds and the turtles have not been seen since (Roberts 1985). The nearest freshwater turtle population is that of *Clemmys marmorata*, which occurs in Arroyo del Rosario approximately 51 km west-northwest (Grismer, unpubl.) and is most likely the species that occurred at Misión San Fernando Velicatá.

Misión Santa María

Misión Santa María [de los Ángeles] is located approximately 17 km east of Cataviña in Arroyo Santa María [=Arroyo Cabujacaamáng] (Fig. 2). This site occurs in a deep canyon within the Vizcaíno Region and is surrounded by extensive granitic outcroppings (Fig. 3). The dominant vegetation of this site consists of the palms *Washingtonia filifera* and *Brahea armata* as well as *Juncus acutus*, sedges, and *Typha domingensis*. Although this site was occupied as the northernmost Jesuit mission from 1767 to 1818, the water course was never altered. Water here is probably only permanently above ground in a few small pools that abut a rock face in the northern corner of the arroyo just below the mission site, but it is much more extensive during periods of precipitation. Cattle have had little impact on this oasis, although their tracks and dung occasionally were found in and around the water. The mesophilic herpetofauna observed here included the California treefrog (*Hyla cadaverina*) and the California striped racer (*Masticophis lateralis*) (Grismer 1993).

Las Palmas

Las Palmas is located approximately 28 km south of Bahía de San Luis Gonzaga in Cañada Tomás along the eastern foot of Mesa Prieta (Fig. 2). This oasis is nothing more than a two meter square hand-dug well at the foot of a basaltic and granitic mesa in the Lower Colorado Valley Region. The water system does maintain a small stand of *Washingtonia filifera*, and the well is surrounded by



Fig. 3. Upper: Misión San Fernando Velicatá. Lower: Misión Santa María.

Typha domingensis. The only mesophilic amphibian found was *Hyla cadaverina*. The presence of this small treefrog suggests that before the alteration of the water source, standing water must have been present for at least some portion of the year allowing the tadpoles of this species to metamorphose. The well was dug to ensure a source of fresh water for the early settlements of nearby Bahía de San Luis Gonzaga and Punta Final. Lately, Las Palmas is intermittently used as a base camp for the illegal hunting of bighorn sheep, mule deer and mountain lion.

Bahía de los Ángeles

Bahía de los Angeles lies on the east coast of the peninsula approximately 150 km south of Bahía de San Luis Gonzaga (Fig. 2) in the Central Gulf Coast Region. Originally, a spring existed above the town at the base of Cerro Bahía de los Ángeles. The spring, which supplied fresh water to the village, was inhabited by *Hyla cadaverina* (SDSNH 47465-73) which were collected there as late as 29 April 1966. We visited this area in July 1991 and found the springs had been replaced with large steel storage tanks into which the town's fresh water is pumped and stored. This pumping has lowered the level of the springs so much that in order to encounter standing water, narrow tunnels have been dug into the ground. As a result, *H. cadaverina* has become extinct in this oasis. Until at least 1966, this area represented the southernmost known locality for this species and the only occurrence of this species in the Central Gulf Coast Region. The southern-most known locality now is at Las Palmas, approximately 135 km to the north.

Misión San Borja

Misión San [Francisco de] Borja [Adác] is located approximately 31 km west-southwest of Bahía de los Ángeles in Arroyo El Ranchito at the northern edge of the Sierra San Borja in the Vizcaíno Region (Fig. 2). It occurs in a wide arroyo basin that is surrounded by volcanic hillsides and mesas. This site was discovered by the Jesuits in 1758 and as early as 1759 construction of stone irrigation works and a chapel was begun. This site was chosen because of its abundant supply of fresh water and, during the Mission Period, there was enough water in this system to cultivate orchards of figs, olives, grapes, and dates as well as fields of wheat, corn, barley, and garbanzos. It is impossible to determine the original condition of this oasis, but certainly there must have been more water than is currently present. The village is still inhabited and the water course is still used for irrigation. The only remaining standing water is in one of the original 12 m by 15 m stone reservoirs which is still in use. Here, several specimens of the Pacific treefrog (*Hyla regilla*) were observed.

Misión Santa Gertrudis

Misión Santa Gertrudis is located approximately 87 km north of San Ignacio in Cañon de Santa Gertrudis (Fig. 2). This site is located in a thickly vegetated, wide, funnel-shaped, rocky arroyo which narrows at its eastern end at the western foot of the Sierra Santa Agueda in the Vizcaíno Region. The dominant vegetation consists of date palms (*Phoenix dactylifera*), *Acacia* sp., and *Washingtonia robusta*. The surrounding foothills are predominantly basaltic; however, the oasis occurs in the midst of a granitic outcrop. This site was discovered by the Jesuits in 1751 and eventually became one of the largest and most successful missions of its time,

which in the mid 1750's supported at least 1400 inhabitants. Consequently, the water system was altered with the construction of stone canals and reservoirs to support cultivation. We visited this site in June 1990 and found the original water system to be in miserable shape. Those few small pools that were present had been heavily trampled and polluted by the urine and dung of livestock. Since this system was extensive enough to support 1400 inhabitants, it certainly must have supported mesophilic amphibians and/or reptiles. It was surprising, however, that no such species were found in this area, suggesting that they must be very rare or extinct because of the severe habitat alteration.

San Francisco de la Sierra

San Francisco de la Sierra is an extensive network of deep branching canyons located approximately 50 km north of San Ignacio in the Vizcaíno Region (Fig. 2). These canyons range in depth from approximately 500 m to 1100 m and in most instances the canyon walls are nearly vertical (Fig. 4). The dominant vegetation in the bottoms of the canyons consists of *Salix* sp. and *Brahea brandegeei*, with *Quercus* sp. occasionally present. We noted extremely high densities of *Hyla regilla* and *Thamnophis hammondi* (*sensu* McGuire and Grismer 1933) in these oases relative to other oases and cismontane areas in both Baja California and southern California. This was by far the most pristine and undisturbed system visited thus far, which is no doubt directly related to its remoteness and inaccessibility. There are goats in the area, but they appear to have had minimal impact.

Sierra Vizcaíno

The Sierra Vizcaíno forms the westernmost continental portion of the Vizcaíno Peninsula of west-central Baja California (Fig. 2). Its close proximity to the cool Pacific currents and continuous onshore breezes leaves it a relatively cool area despite its presence in the Vizcaíno Region. In this mountain range, we found two isolated populations of *Hyla regilla* (Grismer et al. 1993). The first occurred in a shallow rocky arroyo approximately 7 km northwest of Puerto Nuevo. Within this arroyo, both tadpoles and adults were found in a small semi-subterranean pool and a man-made well. Further down the arroyo, adults were found in rock cracks on a shaded, vertical streambed face. The second population occurred in a seepage in a shallow arroyo at Rancho San José de Castro (Fig. 4), where one adult was found and another was heard calling. These frogs represent a range extension of approximately 140 km to the west from their nearest known continental locality of San Francisco de la Sierra. Although the dominant vegetation in these arroyos is composed of xeric Vizcaíno Region species, some relicts of foothill chaparral vegetation of the California Region were found at both localities. *Rhus integrifolia* occurs in the arroyo near Puerto Nuevo and *Malosma laurina* in the arroyo at San José de Castro.

San Ignacio

San Ignacio is located in Arroyo de San Ignacio in the center of Baja California, approximately 59 km west of Santa Rosalía (Fig. 2) on the border of the Vizcaíno and Magdalena Regions. This is an extensive oasis lying in a shallow arroyo bordered by low andesitic volcanic plateaus (Fig. 5). This oasis was discovered by Jesuits in 1716 and became the site of Misión San Ignacio [Kadakaamán] in



Fig. 4. Upper: San Francisco de la Sierra. Lower: Arroyo at Rancho San José de Castro in the Sierra Vizcaíno.



Fig. 5. Upper: San Ignacio. Lower: San José de Magdalena.

1728. Afterwards, this area was heavily cultivated and several plant species were introduced. Although it is one of the most aesthetically appealing oases, it is almost completely unnatural, being shrouded in *Phoenix dactylifera* and bamboo. There are some native palms left in the area but they are by no means dominant. This arroyo has been bisected by a large dam, over which passes a paved road.

The native mesophilic herpetofauna from this area consists of *Hyla regilla*, the slider turtle (*Trachemys scripta*), the endemic Baja California alligator lizard (*Elgaria paucicarinata*), *Thamnophis hammondi*, and *Masticophis lateralis*. Two of the aquatic members of this group, *H. regilla* and *T. hammondi*, occur in very low densities. We believe this is the result of several introduced fishes and the bullfrog *Rana catesbeiana*, which prey on the juveniles and adults of both *H. regilla* and *T. hammondi*. In one large pond west of town, a census estimate made at night on 8 April 1990 averaged one *R. catesbeiana* every three meters along the shore. It was not surprising that *H. regilla* was absent from the pond and restricted to a small irrigation canal along the side of the bank where *R. catesbeiana* were absent.

San José de Magdalena

San José de Magdalena is located approximately 29 km north-northwest of Mulegé in Boca de Magdalena in the Central Gulf Coast Region (Fig. 2). This is a large system of ponds located in a wide, rocky arroyo which is dominated by *Washingtonia robusta* (Fig. 5). Associated with the ponds nearer the town of San José de Magdalena are various species of introduced ornamental trees. Within this system, we observed *Hyla regilla* and *Thamnophis hammondi*. Also present was *Rana catesbeiana*. The Delagado of San José de Magdalena, Octavio Villavicencio Águilas, informed us that *Trachemys scripta* is also present and, along with *R. catesbeiana*, is used as a food source. Although the density of *R. catesbeiana* is high, *T. hammondi* appears to be present in high numbers.

Mulegé

Mulegé is located on the east coast of Baja California approximately 55 km south of Santa Rosalía in the Central Gulf Coast Region at the mouth of Río Mulegé (Fig. 2). This area was first discovered by the Jesuits in 1701 and later became the site of Misión Santa Rosalía de Mulegé. Once again, early cultivation and the introduction of non-native species of plants have left their mark on this water system. For example, *Phoenix dactylifera* dominates the estuarine water course, and covers the adjacent surrounding margins (Fig. 6). The water course extends approximately one km inland where it begins to narrow. Here the ponds have been severely trampled and urinated and defecated in by cattle. This is the most disturbed oasis we visited. In this portion of the oasis, an extremely high density of *Rana catesbeiana* was observed. Specimens of *Hyla regilla* (CAS 136562-83) have been collected and *Masticophis lateralis* (Grismer 1990) and *Thamnophis hammondi* (Mocquard 1899) have been reported, but neither have been observed by us despite several visits. A single specimen of *Trachemys scripta* was observed tethered to a tree in the yard of a house along the water course. The girl to whom the turtle belonged said she caught it in the river. The apparent low densities of *H. regilla* and *T. hammondi* may be due to the presence of introduced fishes.



Fig. 6. Upper: Mulegé. Lower: Cadejé.

La Junta

La Junta is located in Arroyo San José de Gracia on the west coast of Baja California, approximately 58 km south of Laguna San Ignacio in the Vizcaíno Region (Fig. 2). During the dry season, the water at La Junta is contained within a small (ca. 7 m $\times$ 17 m), but deep tinaja in a deep and narrow andesitic arroyo with vertical sides. The dominant vegetation surrounding the tinaja includes *Washingtonia robusta* and *Ficus palmeri*. High densities of *Hyla regilla* tadpoles were observed in the water and adults were observed in the arroyo but no other species were seen. An elderly couple who have ranched this area and utilized the water of this tinaja for nearly 50 years reported that *Trachemys scripta* occurs there, but that there are no *Thamnophis hammondi*.

La Ballena

La Ballena also occurs on the west coast and is located in Arroyo San Raymundo, approximately 20 km south of La Junta in the Vizcaíno Region (Fig. 2). This is an extensive system of water at the bottom of a wide, open, rocky streambed which had very little stream-side vegetation. Despite the abundance of water at this site, no mesophilic amphibians or reptiles were observed. A rancher who lives along the water course reported he had never seen turtles or snakes in the water but gave a very good description of the appearance and behavior of *Hyla regilla*, which he said occurs there. Other ranchers from nearby areas spoke of turtles and snakes also occurring in this system but this remains to be confirmed.

Cadejé

The third oasis visited on the west coast was Cadejé, which consists of three large ponds near the mouth of Arroyo Santa Catarina, approximately 16 km north of San Juanico in the Vizcaíno Region (Fig. 2). There is a small town along this system which uses the water for irrigation and livestock. The dominant vegetation along the water course consists of *Washingtonia robusta*, large stands of bamboo, and a few *Phoenix dactylifera* (Fig. 6). We observed large numbers of *Trachemys scripta*, which are eaten by the locals, and one juvenile *Thamnophis hammondi*. Some children reported that, "(little gray frogs sing from the waters edge at night but that they are hard to find during the day)." This oasis has a high density of introduced fishes which we believe may be the cause of the apparently low numbers of *Hyla regilla* and *T. hammondi*.

Los Burros

Los Burros is located in Arroyo San Gregorio on the west coast of Baja California approximately 17 km west of La Purísima (Fig. 2) in the Magdalena Region. Here the water surfaces from below ground along the edge of a north-facing limestone ridge to form a system of extensive ponds. There is little in the way of stream-side vegetation other than *Juncus acutus* and, despite its large size, only one specimen of *Hyla regilla* was found. This water system has a very high density of introduced fishes which may be the reason for the paucity of other species.

La Purísima

La Purísima is an extensive body of water located at the mouth of Arroyo La Purísima approximately 74 km west-northwest of Loreto in the Magdalena Region

(Fig. 2). This section of the arroyo is very shallow and wide and bordered by heavily eroded small hills of siltstone. The water's edge is cloaked with reeds and the adjacent margins support thick stands of *Phoenix dactylifera* and *Juncus acutus* (Fig. 7). This system was first explored by the Jesuits in 1685 and later settled in 1720 with the founding of Misión La Purísima Concepción [de María] Cadegomó. An irrigation system was established and several crops were introduced and raised, which is the likely origin of the extensive groves of *P. dactylifera*. This oasis is still heavily relied upon by the towns of La Purísima and San Isidro for irrigation, livestock, and drinking water. Although many portions of the stream were heavily polluted by livestock waste during a visit in June 1988 and 1990, *Thamnophis hammondi* were abundant. Also observed were *Hyla regilla* and *Trachemys scripta*.

Comondú Region

The Comondú Region lies in the bottom of Arroyo Comondú, approximately 22 km southeast of La Purísima along the western foothills of the Sierra de la Giganta in the Magdalena Region (Fig. 2). This is a lengthy system composed of numerous small ponds connected by flowing water. The arroyo is in an andesitic canyon that has nearly vertical walls. The dominant vegetation consists of *Brahea brandegeei* and *Phoenix dactylifera* (Fig. 7). This area was first explored by the Jesuits in 1684 and subsequently Misión San José de Comondú was founded in 1708. The mission system brought cultivation to the area along with many introduced species of plants which still persist today. Although this water supports the two small towns of San Miguel de Comondú and San José de Comondú and all their associated agricultural endeavors, the water system is in surprisingly good condition. The mesophilic herpetofauna observed includes, *Hyla regilla*, *Trachemys scripta*, the endemic Baja California skink (*Eumeces lagunensis*), and *Thamnophis hammondi*. The presence of *Elgaria paucicarinata* (Grismer 1988) and *Masticophis lateralis* (Jennings 1983; Grismer 1990) have been previously reported.

Las Parras

Las Parras is a small water system located within the narrow and sinuous Arroyo Las Parras, approximately 15 km southwest of Loreto in the Central Gulf Coast Region (Fig. 2). The dominant vegetation consists of *Brahea brandegeei* and *Juncus acutus*. During the dry season, water may be found only at the establishment of Las Parras. However, during periods of seasonal precipitation, a system of ponds exists which continues eastward a short distance down the arroyo toward the Gulf of California. In these ponds, several individuals of *Hyla regilla* were observed, and although the pools were sufficiently large to support *Thamnophis hammondi* during a visit in July of 1990 and 1991, none were observed. The local inhabitants at Las Parras told us that snakes and turtles do not occur in the water there.

Misión San Javier

Misión San [Francisco] Javier [Viggé Biaundó] is located in Arroyo de San Javier approximately 28 km south of Loreto (Fig. 2) in the Arid Tropical Region of the Sierra de la Giganta. The oasis system lies at the foot of a large andesitic



Fig. 7. Upper: La Purísima. Lower: Comondú Region.

mesa and there is little in the way of palms or stream-side vegetation (Fig. 8). This site was first discovered by the Jesuits in 1699 and a mission was founded later that same year. Stone dams and canals were constructed to divert water for irrigation purposes, although little in the way of introduced plants have persisted. Currently, there is a large stone dam just east of the mission creating a large deep pond which supports the small town and a few ranchos. The mesophilic herpetofauna observed included *Hyla regilla*, *Trachemys scripta*, and *Thamnophis hammondi*. *Hyla regilla* and *T. hammondi* occurred in very low numbers and, in fact, only a single individual of each species from this oasis was seen. This is probably due to the extremely high density of introduced fishes.

La Presa Region

The La Presa Region is an extensive system of at least three separate drainages located approximately 120 km north of the Isthmus of La Paz in the Arid Tropical Region of the Sierra de la Giganta (Fig. 2). Within this region there are many canyons and oases, most of which are associated with at least one rancho. There is a great diversity in size and shape of these oases. Some are shallow and wide, others are narrow and deep, some are nothing more than muddy ponds along a bend in the arroyo, and some support seven to 10 m high waterfalls (Fig. 8). A few of the oases we visited have been dammed but the majority have been left in a natural state. The associated vegetation along these oases is as variable as the oases themselves. Much of it along some of the older and larger establishments, such as that of San Pedro de la Presa, is composed of introduced ornamentals. At other sites, such as at Rancho Purificación, in a different drainage system, the associated vegetation is natural with species such as *Salix* sp., *Brahea brandegeei*, and *Ficus palmeri* being dominant. Without a doubt, ponds occurring in the same arroyo are confluent during the rainy season of mid-July to September allowing for dispersal and gene flow of aquatic and semi-aquatic species along these corridors. Eleven localities were visited within two separate drainage systems (Table 1) and nearly all of them had *Hyla regilla*, *Trachemys scripta*, and *Thamnophis hammondi*. Grismer (1988) reported on a specimen of *Elgaria paucicarinata* from this region.

Discussion

The general pattern that emerges from this study is that the majority of these oases usually have a treefrog (*H. regilla* in most cases), *Trachemys scripta*, and *Thamnophis hammondi* (Table 2). The most common species found throughout the oasis system was *Hyla regilla* which occurred in all but four of the oases examined. In the four oases from which this species was absent, *H. cadaverina* was present in all except Misión Santa Gertrudis, where no treefrogs were found. In many cases, additional nonaquatic mesophilic taxa such as *Eumeces lagunensis*, *Elgaria paucicarinata*, and *Masticophis lateralis* are found in association with the oases. In actuality, it is believed that these species, and perhaps additional mesophilic forms, occur in most of these oases (the exception being the absence of *Trachemys scripta* north of San Ignacio) but have not yet been found. All are somewhat secretive and very swift and/or agile which makes observation difficult. In fact, in those oases where these species were observed, it was fortuitous rather

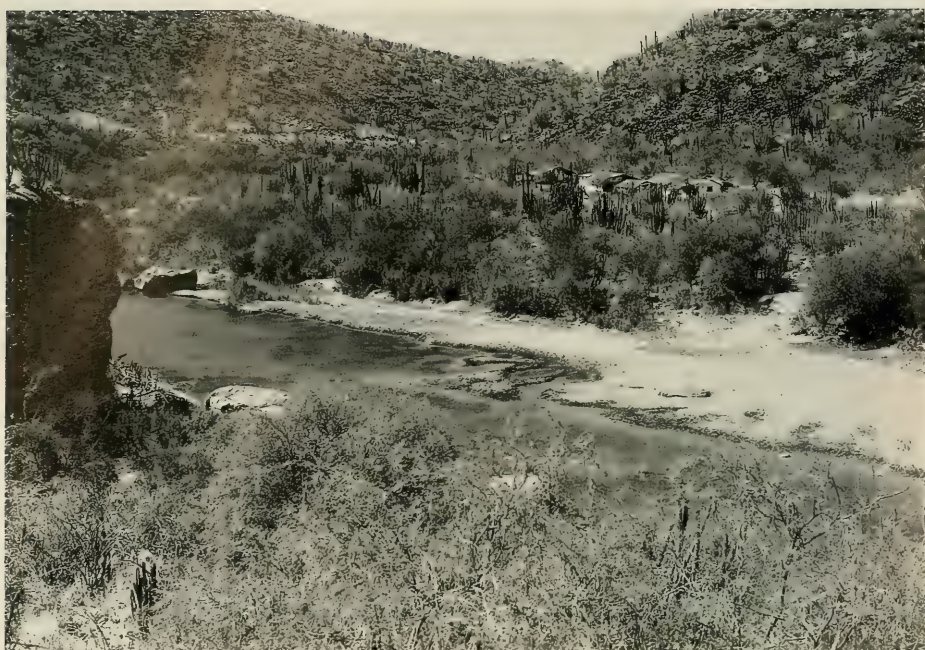


Fig. 8. Upper: Misión San Javier. Lower: Rancho La Purificación (west) in Arroyo Primer Agua of the La Presa Region. Note the presence of the waterfall in the center of the photograph.

Table 1. Oases visited in five different arroyos in the La Presa Region (Fig. 1). Arroyos El Bosque, Primer Agua, and La Soledad are connected and form a single branching system separate from Arroyos Las Animas and La Presa which are connected and form a different system.

Arroyo El Bosque
Rancho El Bosque
Rancho La Purificación (east)
Arroyo Primer Agua
Rancho La Purificación (west)
Arroyo La Soledad
Rancho Los Paredes
Pond 1.5 km west (by dirt road) of Rancho Las Paredes
Pond 2.1 km west (by dirt road) of Rancho Las Paredes
Pond 4.3 km west (by dirt road) of Rancho Las Paredes
Rancho El Portrero
Arroyo Las Animas
Las Animas
San Pedro de La Presa
Arroyo La Presa
Rancho La Presa

than by design. Therefore, the species lists for these oases (Table 2) likely underestimate the number of taxa actually present.

Trachemys scripta is absent from areas north of San Ignacio because, in part, there are no water systems large enough to support this species, with the exception

Table 2. Species observed or reported as present in the literature (×) and reported as present by ranchers (R). Localities listed in order of north to south. † indicates extinction; ? indicates the species was not observed or reported but expected.

	<i>Hyla cada-verina</i>	<i>Hyla regilla</i>	<i>Rana cates-beiana</i>	<i>Trache-mys scripta</i>	<i>Clem-mys mar-mo-rata</i>	<i>Eumeces lagun-ensis</i>	<i>Elgaria pauci-cari-nata</i>	<i>Masticophis later-alis</i>	<i>Thamnophis ham-mondii</i>
Misión San Fernando Velicatá	×	×			†				×
Misión Santa María	×							×	
Las Palmas	×								
Bahía de los Ángeles	†								
Misión San Borja		×							
Misión Santa Gertrudis									
San Francisco de la Sierra		×							×
Sierra Vizcaíno		×							
San Ignacio		×	×	×			×	×	×
San José de Magdalena		×	×	R					×
Mulegé		×	×	×				×	×
La Junta		×		R					
La Ballena		R		?					?
Cadejé		R		×					×
Los Burros		×							
La Purísima		×		×					×
Comondú Region		×		×		×	×	×	×
Las Parras		×							
San Javier		×		×					×
La Presa Region		×		×			×		×

of San Francisco de la Sierra. Conant (1969) and Murphy (1983) suggested that *Trachemys scripta* may have been introduced into Baja California by native Indians and/or Jesuit Priests (Murphy 1983) as a food source. If so, the founder population would have had to have come from southern Sonora-northern Sinaloa where the closest relative of *T. s. nebulosa* (the Baja California form), *T. s. hiltoni* (Legler 1960, 1990; Legler and Webb 1970) occurs. There is only weak evidence at best, however, of transgulfian migrations of native Indians into Baja California from mainland México and no evidence of permanent residency (Aschmann 1959; Laylander 1987). Additionally, the people who made these questionable journeys were the Seri Indians (Laylander 1987) in the midriff region of the Gulf of California, far to the north of where *T. s. nebulosa* and *T. s. hiltoni* are found. Thus, it is believed here that an introduction from native Indians is unlikely.

Clavijero (1789) discussed the turtles of Baja California in *Storia della California* and stated that "[Among the turtles, besides the common land variety and the fresh-water ones, there are two other species of large sea turtles]." This statement not only implies that testudinids were present in Baja California before 1789 (see Crumly and Grismer [1992] for further discussion) but that freshwater species were also present. Although Clavijero was never in Baja California, he had access to all classified documents, many of which are no longer in existence, and corresponded first hand with many of the Jesuits that were in Baja California. Clavijero was heralded as a literary genius who wrote accurately and impartially. Therefore, it is unlikely that the mention of terrestrial and freshwater turtles is a fabrication on his part. No mention, however, is made of nonmarine turtles being a food resource in other extant Jesuit literature. Even Johann Jakob Baegert, who lived with the Guyacura Indians at Misión San Luis Gonzaga and wrote extensively of their food habits (Baegert 1772), made no mention of non-marine turtles being eaten. However, *T. s. nebulosa* occurs in this region today and is eaten by the local inhabitants. If this species was introduced by Jesuits from mainland México as a food source, as has been suggested (Murphy 1983), it is reasonable to assume that its consumption would have been reported in Jesuit literature as was the consumption of all the other foods they imported. It is more probable that *T. s. nebulosa* had a natural origin in Baja California that is related to the tectonic evolution of the peninsula (Grismer 1992). It is likely that it has been recently transported throughout southern Baja California as a food source and introduced into water systems large enough to support it. Such introductions still occur in the Cape Region. The presence of this species in La Presa de la Buena Mujer, a newly constructed dam just south of La Paz, is evidence of this. In some of the more remote areas of southern Baja California, such as the La Presa region and some of the ranchos southwest of San Ignacio, *T. scripta* is a food source and their shells are conspicuous components of the garbage scattered around the ranchos. This would explain their presence at San Ignacio and their absence at San Francisco de la Sierra. The water systems on San Francisco de la Sierra are far from the ranchos and the small community on the surrounding terraces and accessed only by a day's journey by burro down exceedingly steep cliffsides.

The historical transformation of central Baja California from a more mesic region in the Pliocene to a xeric region has been well documented, using both paleobotanical (Axelrod 1979; Van Devender and Spaulding 1979; Van Devender 1990; Wells 1969) and paleovertebrate (Miller 1977; Van Devender 1990) evi-

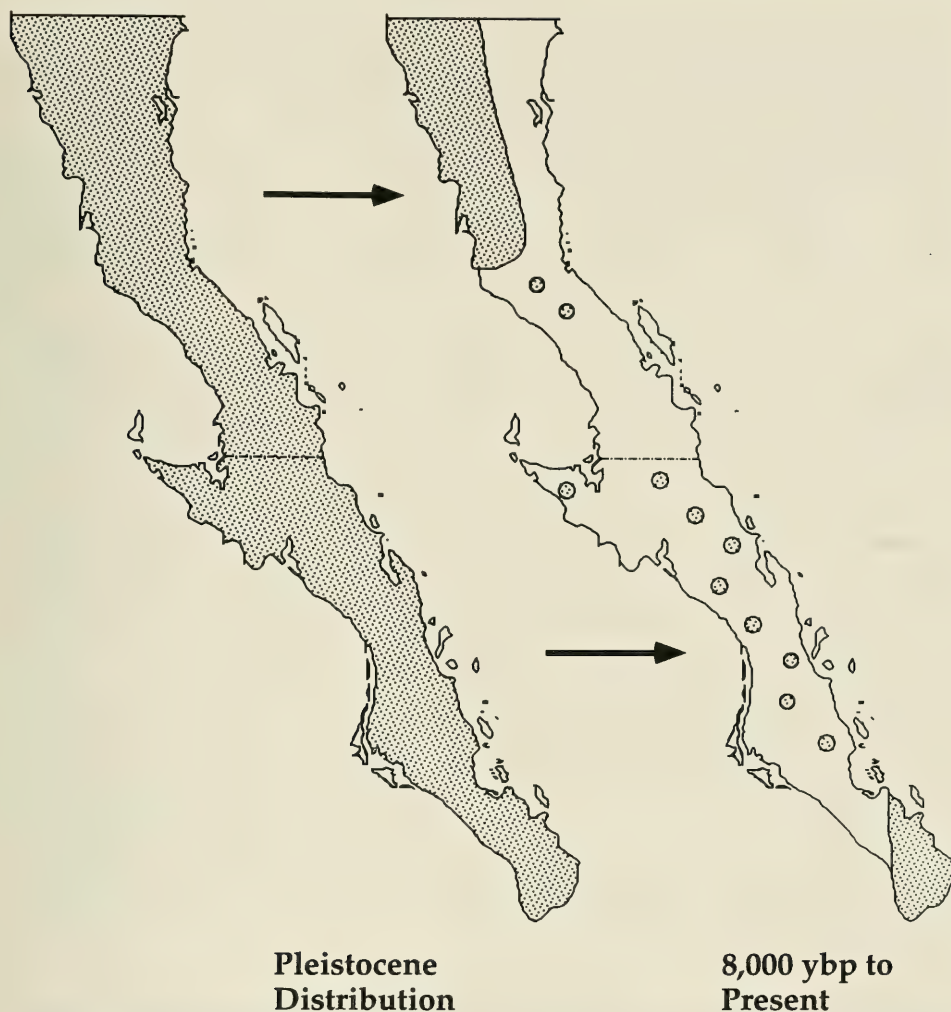


Fig. 9. Generalized historical and contemporary distribution of the mesophilic herpetofauna of central Baja California.

dence. This transformation was slow at first but at approximately 8000 to 10,000 years before present it became very rapid. The documentation of mesophilic amphibians and reptiles from the oases of central Baja California provides additional evidence supporting the occurrence of a drying trend. Because of the mesophilic habits of these taxa, they would not naturally disperse across wide expanses of open desert to reach these oases today. Therefore, they probably always were present in the areas but, because of desertification, have become isolated. Thus, we are proposing that these taxa probably had prior continuous transpeninsular distributions but with the formation of mid-peninsular deserts became restricted to these disjunct mesic outposts (Fig. 9). Such scenarios have been suggested previously for members of this herpetofauna (Grismer 1988, 1990, 1992, 1993; Grismer et al. 1993; McGuire and Grismer 1993), as well as for mountain top relicts (Grismer and Mellink 1994).

Some of these oases are in varying stages of disruption as a result of direct and indirect human alteration. The direct physical alteration of the Bahía de los Ángeles oasis has resulted in the recent extinction of the southernmost population of *Hyla cadaverina* and a similar situation may have occurred at Misión San Borja for other species. The most heavily impacted oasis may be that at Misión Santa Gertrudis, where the introduction of livestock and cultivation may have made the water system in this area uninhabitable and caused the extinction of an entire mesic herpetofauna. A similar situation is occurring at Mulegé and La Purísima; however, as of yet, the water system of the latter is so extensive, human impact appears to be accommodated. Unfortunately, the main road from Ciudad Insurgentes to La Purísima recently was paved which will undoubtedly result in increased travel to this area and eventually an increase in the population. This will, in turn, increase the demand on the water system.

In addition to the physical alteration of these water systems, is the biological alteration resulting from the introduction of nonnative species of plants and animals. Many of these introductions began during the Mission Period, and are now so well-established that they have irrevocably altered some of these systems. San Ignacio and Mulegé seem to be the best examples of this. Currently, their stream-sides are cloaked in bamboo and date palms and their waters filled with bullfrogs and various species of introduced fishes. This apparently contributes to the low density of some of the native herpetofauna. The introduction of non-native fishes is having similar effects at Misión San Javier, Los Burros, and Cadejé.

It is not known whether such damage can be mitigated but we do believe that something should be done to insure that no further damage is levied on those oases that have been altered and that nearly pristine areas, such as San Francisco de la Sierra and some places in the La Presa Region, remain unaltered. There are many reasons why these systems should be protected from further degradation, one of the most important of which may be that these areas are truly living windows through which one can look into the past.

Resumen

La porción central de la península de Baja California ha pasado por una transformación ecológica de una área mojada, apoyando una flora y fauna mesófila a una área xerófila, que apoya plantas y animales de regiones áridos. Esta transformación ha dejado muchos lugares relictas y mesófilos que corrientemente están rodeados por desierto. Estes lugares ocurren principalmente en la forma de oases que también tienen una herpetofauna relictas y mesófila. El patrón se observa más frecuentemente es que las mayorías de los oases tienen, por lo menos, una ranita (usualmente *Hyla regilla*), una tortuga (*Trachemys scripta*) y una culebra del agua (*Thamnophis hammondi*). También, hay otras especies que se encuentran de vez en cuando así como la ranita (*Hyla cadaverina*), el síncido endémico de Baja California (*Eumeces lagunensis*), el ajolote de cuatro patitas (*Elgaria paucicarinata*), y la sinturiata de California (*Masticophis lateralis*). La ocurrencia de estas especies en estos oases apoya el hipótesis de una transformación ecológica de un período más mojado de lo que existe hoy. Esto es por que estas especies no podrían dispersar a través expansas amplias de desierto abierto para alcanzar estos oases. Por lo tanto, habrían estado allí antes de la formación del desierto y entonces, ellas son verdaderamente relictas.

La condición de los oases varían. Algunos, como el de San Francisco de la Sierra y algunos del Region de La Presa, son muy prístinos y impertubados. Por el otro lado, algunos como el de Bahía de los Ángeles, está arruinado y la herpetofauna asociada es extinta. Mucha de la alteración humana de los oases ha continuado desde la presencia de las misiones y continúa corrientemente. La introducción de plantas y animales nuevos ha contribuido y continúa contribuir a la degradación de estas sistemas. Medidas deben estar realizadas para impedir destrucción adicional.

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Megabenthic Assemblages of Coastal Shelves, Slopes, and Basins off Southern California

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Abstract.—Megabenthic invertebrate assemblages from soft sediments on the mainland shelf and San Pedro and Santa Monica Basin slopes and floor were identified based on 1203 otter trawl collections made between 1971 and 1985 at depths ranging from 10 to 915 m. Major changes in species composition and abundances occur at mid-slope (~300 m) and at the basin sills (~715 m). The mainland shelf assemblage (10–137 m) is dominated by the sea urchin *Lytechinus pictus* and the prawn *Sicyonia ingentis*. This assemblage is heterogeneous in space and time, with sub-assemblages that reflect severe contamination and large storms and/or El Nino. The basin slopes are dominated by the echinoids, *Allocentrotus fragilis*, *Brissopsis pacifica*, and *Brisaster latifrons*. The latter two species may exist in kilometer scale herds on the slopes, but they are absent below the basin sills (737 m). Galatheid crabs are the most abundant megafauna in the San Pedro and Santa Monica Basins. Species composition of all assemblages appeared to be seasonally stable, but *S. ingentis* and the tuna crab *Pleuroncodes planipes* increased by several orders of magnitude during El Nino. Numbers of megafaunal species, individuals, and biomass were highest on the basin slopes reflecting elevated levels of organic material in the sediment. Numbers of individuals and biomass increased on the lower slopes (500–800 m), following El Nino. Although organic material is highest in the basins, the numbers of species and individuals were much lower than on the lower slopes. Near anaerobic conditions in the basins probably exclude many species.

The large invertebrates that inhabit soft sediments on the sea floor are the most obvious biological component of the benthos and usually contribute most to benthic community biomass (Haedrich et al. 1980; Smith and Hamilton 1983). Megabenthos are usually defined operationally (e.g., Rex 1981), and in this paper they are animals larger than 4.2 cm, the mesh size of the otter trawl net used for sampling. Megabenthos are different from macrobenthos in size and species composition. Macrobenthos are usually collected with grab or core samplers and are defined as animals retained on a 0.5 mm sieve. While there may be some overlap in the kinds of animals collected by grabs, corers, and trawls, the species collected by trawling are usually quite different due to differences in animal size, motility, and population dispersion.

The purpose of this study was to determine spatial and temporal patterns in megabenthic species composition, abundances, and biomass from otter trawls collected on the mainland shelf and from the San Pedro and Santa Monica Basin

slopes and floors off southern California. Megabenthos have been collected for decades off southern California, but no synthesis of their assemblage patterns in space or time has been conducted.

Along the coast of southern California, soft sediments (unconsolidated gravels through clays) are the predominant substrata in most areas deeper than about 30 m. From the shallow subtidal to the basin floors, average sediment grain-size decreases from coarse sand to fine clayey-silt, and organic material increases from less than 1% to more than 6% (Emery 1960; Anderhalt and Reed 1978). Dissolved oxygen concentrations near the seafloor decrease to below 1 mg l^{-1} near mid-slope ($\sim 350 \text{ m}$), and to 0.1 mg l^{-1} or lower on the nearshore basin floors (Emery 1960; Minard 1968). These strong environmental gradients are reflected in macrofaunal zonation over depth (Thompson and Jones 1987) and may also be expected to influence the megabenthos.

Additionally, long term temporal variation of megabenthos is unknown. During this study, episodic events such as large storms and El Nino occurred off southern California in 1982–1983. El Nino brings warmer water ($16\text{--}23^\circ\text{C}$) into the region affecting kelp (Dayton and Tegner 1984), and fish abundances (Cross and Allen in press). Other events such as periodic oxygen depletion and renewal in the nearshore basins, and decreases in sewage discharge, also occurred. As will be shown, these events may also affect megabenthic species composition and abundances (Cross and Allen in press).

Methods

The data used in this study were compiled from 1203 otter trawls collected at 262 sites (Fig. 1). These trawls were collected over 15 years, 1971–1985, at depths between 10–915 m (Table 1).

Most of the trawls were collected as part of monitoring programs by several agencies (Table 1), thus trawling was conducted at different times and depths. Between 1971 and 1976 only the area off the Palos Verdes peninsula (PV) was sampled. Beginning in 1976, additional areas throughout the region were sampled. Most trawls (803) were from mainland shelf depths. These include 2 large surveys of the entire mainland shelf in 1977 (Word and Mearns 1979) and 1985 (Thompson et al. 1987b). Deeper slope and basin sites were only sampled a few years, and each of the sub-sill basin sites were only sampled once.

An otter trawl with 7.6 m headrope, 4.2 cm mesh (stretched) net with a 1.3 cm mesh cod-end liner was used. All trawls were made for 10 min (estimated bottom time) parallel to the isobaths, at ship speed of 2 kts, with a scope ratio of 2–4:1; the distance trawled was about 0.5 km, roughly 2285 m^2 .

Trawling is known to produce biased data due to catch selectivity, and generally underestimates abundances (Pereyra and Alton 1972; Haedrich et al. 1975; Rex 1981). In the present study, all trawling was conducted using the same type of gear and in the same manner. Therefore the catches are comparable, but since the data may be imprecise, catches are expressed as numbers per trawl rather than absolute densities.

The trawl collected some macrobenthic and juvenile megabenthic animals smaller than 4.2 cm along with the larger megabenthos. Although all animals caught were identified, midwater and macrobenthic animals were not included in this analysis. Only species considered to be megabenthic (both small and large specimens) were

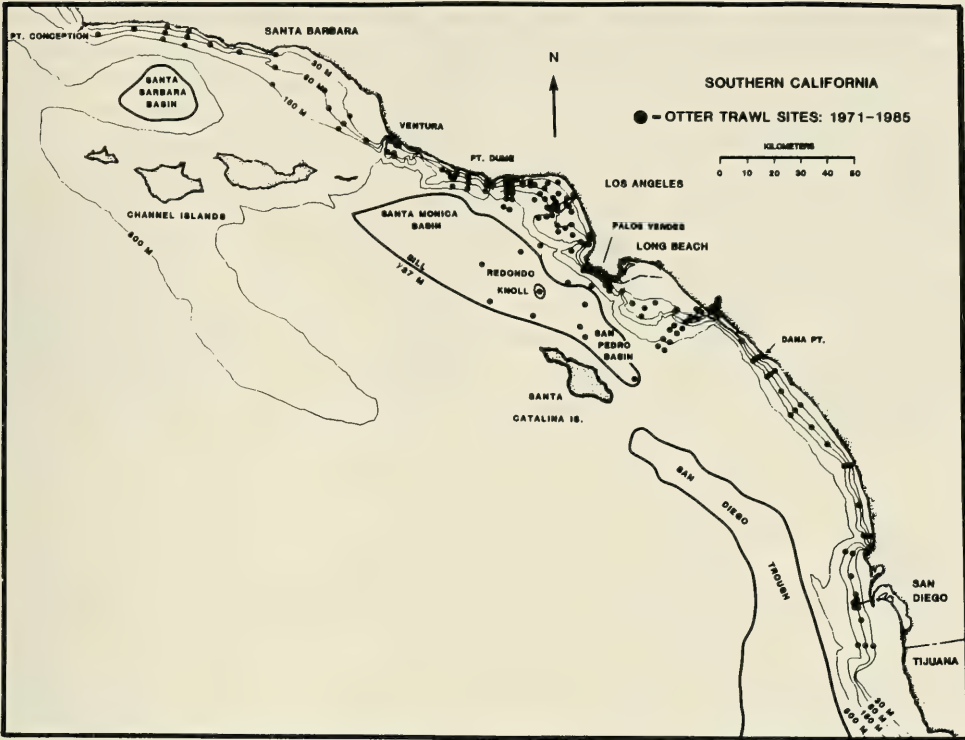


Fig. 1. Chart of southern California coast showing locations of otter trawls collected between 1971–1985.

included. However, single occurrences and taxa above genus were omitted unless they were monospecific or deemed essential for the interpretation of the data. A total of 191 megabenthic species were used in the analysis.

Identification of megabenthic assemblages in space and time was accomplished

Table 1. Sources of data used in this study. CSDOC = County Sanitation Districts of Orange Co., LACSD = Los Angeles County Sanitation Districts, LAOMA = Los Angeles-Orange Co. Metropolitan Area, LARWQCB = L.A. Regional Water Quality Control Board. * indicates data from waste discharge monitoring reports by the agency referenced.

Area-Survey	No. of sites	No. of trawls	Depths (m)	Years	Reference
Ventura-Oxnard	18	19	14–300	1978–82	City of Oxnard*
Santa Monica Bay	66	82	10–300	1977–84	Hyperion Treatment Plant*
Palos Verdes Pen.	35	617	23–137	1971–84	LACSD*
Orange County	12	276	18–137	1976–84	CSDOC*
San Diego	12	59	60–80	1978–84	City of San Diego*
60 m survey	52	52	60	1977	Word and Mearns 1979
Reference survey	38	38	30–150	1985	Thompson et al. 1987b
CSDOC DEEP	16	48	300–627	1981–83	Thompson et al. 1984
LAOMA	8	8	549–915	1977	Mearns et al. 1978b
LARWQCB	4	4	780–877	1985	SCCWRP unpubl.
Totals	261	1203	10–915	1971–85	

using ordination and classification analyses (Clifford and Stephenson 1975; Smith et al. 1988). Due to the large size of the species-sites data matrix, it was necessary to "telescope" the data into groups of sites with similar species composition and abundances using several steps: 1) An ordination space was constructed using detrended correspondence analysis (DCA; Hill and Gauch 1980) of transformed (square root) and standardized (species mean) species abundances. 2) The ordination scores were clustered arbitrarily into 40 groups using SAS FastClus (SAS 1985). 3) A representative "nodal" site in the center of each of the 40 groups in the ordination space was selected. Then the euclidian distance of each site in the group to the nodal site was calculated to generate mean species distances in each nodal group. 4) Using the mean distances, Bray-Curtis similarity index values were calculated. The nodal groups were classified using ecological distance (1 minus similarity), and clustered using agglomerative hierarchical clustering (Smith et al. 1988).

Results

Patterns of Species Composition and Abundance

Ordination and classification analyses revealed 7 site groupings that represent major megabenthic assemblages with different species composition and abundances (Fig. 2). The main groupings were related to water depth: the two main branches of the dendrogram separate lower slope and basin sites (479–875 m) from shelf, upper slope, and mid-slope sites (10–490 m). The shallower branch was secondarily divided between shelf and slope depth sites. The shelf depth sites were further separated into groups that represent spatial and temporal variations of the normal mainland shelf assemblage. One small cluster was formed by 7 sites from shelf depths that were "short" trawls with abnormally low catches (15–17 organisms). These sites will be disregarded.

Temporal differences in species composition and abundances in the assemblages occurred only at some of the mainland shelf sites, forming sub-assemblages. Samples collected at various times from the other major assemblages were consistently classified together and showed no seasonal (winter, summer) or longer term changes in overall species composition (Fig. 2). Differences in species composition or abundances would have formed separate site groupings as they did for the mainland shelf assemblages. However, abundances of several individual species were highly variable over time as will be shown below.

Mainland shelf.—The megabenthos on the mainland shelf between the depths of 10–137 m forms a large scale assemblage that extends from Pt. Conception to Mexico. The most common and abundant species in this assemblage are listed in Table 2. Samples from all years between 1971 and 1985 were included in this group (Fig. 2). The low frequencies of occurrence in catches of many species reflect both patchy distributions of these animals, and variations in their abundances over time.

The most abundant species on the mainland shelf is the white urchin *Lytechinus pictus*. They are most abundant at depths between 40–60 m, but were collected to 205 m. Their presence in only 45% of trawls on the shelf reflects their heterogeneous distribution in both space and time. Abundances of *L. pictus* varied by orders of magnitude at different depths and in different years (Fig. 3). Abundances

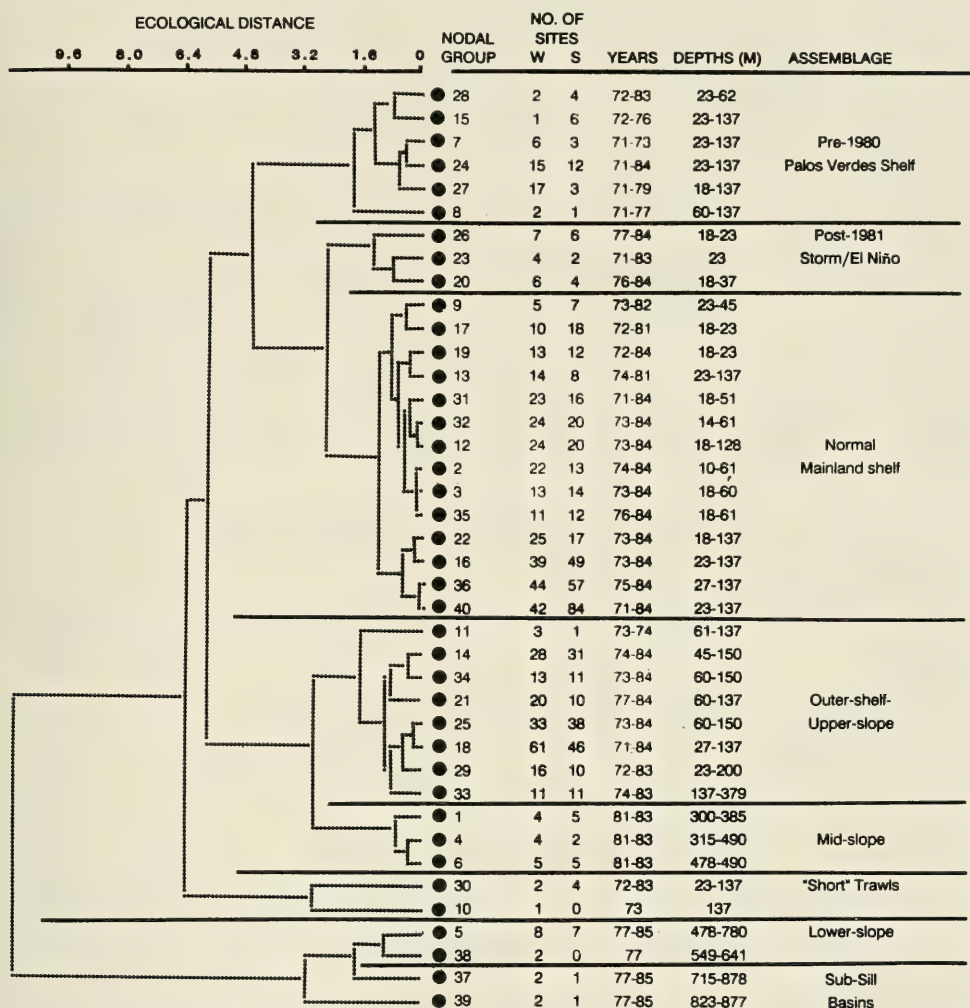


Fig. 2. Dendrogram from classification analysis of otter trawl data. Nodal groups and ecological distance are explained in the text.

at depths shallower than 50 m peaked in 1979. Abundances at 51–100 m peaked in 1981, then decreased in 1982, during the storms and El Niño. By 1985 mean abundances decreased to less than 100 trawl⁻¹ at all depths. Factors that may cause the peaks in abundance are not known.

This species often forms "herds" on the shelf, but solitary individuals may also be collected. Based on grab and box core samples, the herds may be up to $50 \times 10^3 \text{ m}^2$ in size, and are usually composed of several age classes. Average population densities on the shelf range up to 12 m⁻², but within herd densities are probably much higher (Fauchald and Jones, 1979; SCCWRP unpubl).

L. pictus also inhabits the Channel Island shelves, and offshore ridges and banks off southern California where they are even more abundant than on the mainland shelf (up to 110 m⁻²) and may range deeper (to 390 m; Fauchald and Jones 1983).

Table 2. Mean abundance (frequency of occurrence) per trawl of the most common and abundant species in each assemblage. This table includes the 5 most abundant and the 5 most frequently collected species in each site group. The species are listed in the order determined by inverse (R mode) classification. + = present, R = <1 per trawl. c = crustacean, m = molluscan, e = echinoderm, cn = cnidarian.

Species	Assemblage:		Post-1981 storm, El Nino 18-37 29	Normal mainland shelf 10-137 658	Outer shelf-upper slope 45-315 343	Mid- slope 300-490 25	Lower slope 478-780 17	Basins 715-878 6
	Depth range (m): No. of trawls:	Pre-1980 Palos Verdes 23-137 78						
Taxon								
<i>Paguristes ulreyi</i>	(c)	0	.9 (.24)	.2 (.40)	.02 (.10)	0	0	0
<i>Kelletia kelletii</i>	(m)	.03	.9 (.07)	.2 (.08)	.02 (.02)	0	0	0
<i>Cancer gracilis</i>	(c)	.8 (.16)	0	.5 (.16)	.08 (.05)	0	0	0
<i>Portunus xantusii</i>	(c)	.06 (.03)	2 (.55)	.7 (.09)	.03 (.03)	0	0	0
<i>Heterocrypta occidentalis</i>	(c)	.04 (.03)	.6 (.28)	1 (.26)	.04 (.02)	0	0	0
<i>Astropecten verrilli</i>	(e)	.2 (.09)	7 (.62)	39 (.79)	33 (.45)	0	0	0
<i>Cancer anthonyi</i>	(c)	.9 (.34)	.03 (.03)	.2 (.06)	.1 (.07)	0	0	0
<i>Mursta gaudichaudii</i>	(c)	5 (.59)	.07 (.03)	1 (.33)	11 (.60)	0	0	0
<i>Pleurobranchaea californica</i>	(m)	3 (.47)	.03 (.03)	2 (.40)	8 (.68)	1 (.32)	0	0
<i>Lytechinus pictus</i>	(e)	4 (.05)	85 (.52)	414 (.45)	88 (.23)	0	0	0
<i>Arcoscalpellum californicum</i>	(c)	.01 (.01)	0	.5 (.38)	.2 (.19)	0	0	0
<i>Parastichopus californicus</i>	(e)	2 (.14)	.03 (.03)	8 (.38)	12 (.53)	.2 (.12)	0	0
<i>Crangon alaskensis</i>	(c)	.9 (.09)	.03 (.03)	3 (.36)	18 (.54)	1 (.08)	.12 (.06)	0
<i>Sicyonia ingentis</i>	(c)	5 (.22)	.2 (.01)	74 (.64)	782 (.88)	0	0	0
<i>Pleuroncodes planipes</i>	(c)	.04 (.03)	.4 (.07)	16 (.03)	662 (.11)	0	.4 (.12)	0
<i>Pandalus jordani</i>	(c)	1 (.01)	0	.01 (R)	68 (.17)	.04 (.04)	0	0
<i>Allocentrotus fragilis</i>	(e)	0	0	.2 (.03)	83 (.36)	391 (.96)	.8 (.06)	0
<i>Brisaster latifrons</i>	(e)	0	0	R	9 (.13)	362 (.88)	2 (.29)	0
<i>Brissopsis pacifica</i>	(e)	0	0	R	17 (.06)	3919 (1.0)	1225 (.94)	0
<i>Pannychia mosleyi</i>	(e)	0	0	0	R	16 (.60)	49 (.88)	0
<i>Myxoderma platyacanthum</i>	(e)	0	0	0	0	127 (.60)	473 (.82)	0
<i>Ophiomusium jollienensis</i>	(e)	0	0	0	0	8 (.60)	82 (.88)	0
<i>Ophiocolex corynetes</i>	(e)	0	0	0	0	.2 (.12)	849 (.24)	0
<i>Asteronyx longifissus</i>	(e)	0	0	0	0	7 (.48)	843 (.71)	0
<i>Bathybembix bairdii</i>	(m)	0	0	0	0	0	35 (.88)	.5 (.17)

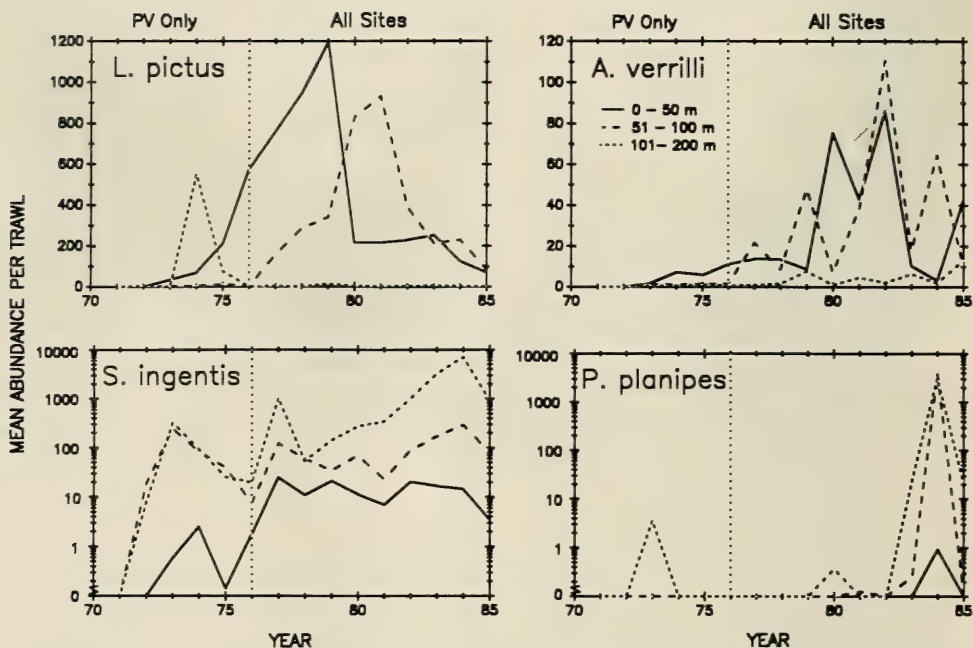


Fig. 3. Mean abundances of some of the most abundant megabenthic species on the mainland shelf at different depths and years. Vertical line at 1976 separates data from off Palos Verdes only and data from all areas of the region.

They may aggregate in kelp beds where they can grow to much larger sizes than those collected in trawls on the shelf (Dean et al. 1984; Coyer et al. 1987).

The asteroid *Astropecten verrilli* was the most commonly collected megabenthic species in the normal mainland shelf assemblage (frequency of occurrence = 79% of trawls, Table 2). They were most abundant at depths around 90 m, but were collected to 205 m. Their abundances were extremely variable and large catches are occasionally made at sites shallower than 50 m (Fig. 3). The largest catches were in 1982 when the storms and El Nino occurred.

Before 1980, megafaunal species composition and abundances on the mainland shelf of the Palos Verdes (PV) peninsula were different from the normal mainland shelf assemblage and formed a separate sub-assemblage (Fig. 2). All of the species in the sub-assemblage were also members of the normal mainland shelf assemblage but most occurred in reduced abundances, and many normal shelf species were not collected in this assemblage (Table 2). The decapod *Mursia gaudichaudii* was the most abundant species, and the opisthobranch *Pleurobranchaea californica*, *L. pictus*, and the ridgeback prawn *Sicyonia ingentis* were among the most common and abundant species in this sub-assemblage. *L. pictus* occurred in greatly reduced abundances compared to the normal shelf sites. This species is very sensitive to contamination. Contaminated sediments near the PV outfall caused decreased growth and gonad production in this species (Thompson et al. 1989).

The number of sites classified in the pre-1980 PV assemblage decreased over time (Fig. 4). In 1971, 72% of the trawls off PV were classified in that assemblage. By 1975, less than 10% of the trawls collected off PV were classified in that group, and after 1980 only 2 trawls were classified in that group.

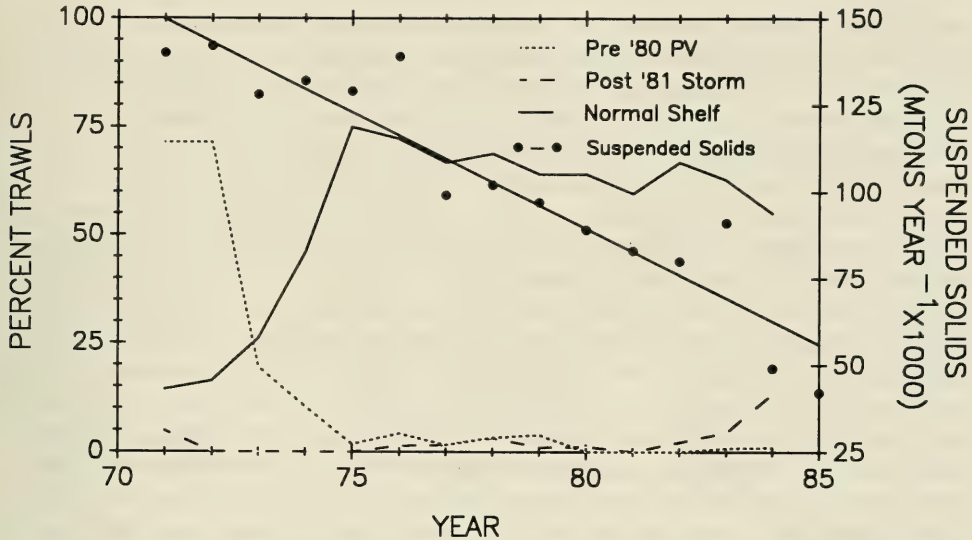


Fig. 4. Percentages of trawls classified in the normal mainland shelf and shelf sub-assemblages each year. Data include all shelf depth sites 10–137 m. Trends in annual mass emissions of suspended solids from PV outfall are also shown (data courtesy of Los Angeles Co. Sanitation Districts).

The existence of this sub-assemblage during the 1970's corresponds to a period of severe sediment contamination from the Los Angeles County Sanitation District's (LACSD) sewage outfall which discharged over 140×10^3 mtons yr^{-1} of suspended solids (particulate material resistant to sewage treatment) on the PV shelf. During this study, improved treatment and source control programs greatly reduced the amount of suspended solids discharged from the outfall (Fig. 4). A direct relationship between suspended solids emissions and altered benthos was shown by Mearns and Word (1982), and the demise of the pre-1980 PV sub-assemblage may also be related to decreased solids emissions.

Below emission rates of about 130×10^3 mtons yr^{-1} of suspended solids, normal megabenthos began to inhabit the area. By 1980, the benthic habitat off PV had apparently improved and the samples collected there were usually classified with the normal mainland shelf assemblage.

Another sub-assemblage of the normal mainland shelf assemblage occurred only at the shallowest shelf sites (18–37 m) between 1982–1984 (Fig. 2). Sites from Palos Verdes, Santa Monica Bay, and Orange County were included in this sub-assemblage, but none of 7 sites sampled off Ventura were included. Prior to 1982, only a few sites were occasionally classified in this sub-assemblage, but by 1984, 19% of the mainland shelf sites were classified in this group (Fig. 4). This increase corresponds with severe winter storms and El Nino that occurred in 1982.

As in the pre-1980 PV assemblage, there were no species unique to this sub-assemblage. The most common and abundant species, *L. pictus* and *A. verrilli*, were also dominant in the normal mainland shelf assemblage, but were collected in reduced abundances in this assemblage. Other species such as the anomuran crab *Paguristes ulreyi* and the brachyuran crab *Portunus xantusii* were more common and abundant than in the normal shelf group. The latter species is a warm water crab, normally with a more southern distribution (Garth and Stephenson

1966), thus its occurrence in this sub-assemblage may be related to El Nino. However, since this group was only composed of shallow sites, we presume that disturbance from the high surf accompanying the storms of 1982 was also responsible for creating this sub-assemblage. It is not possible to determine whether storm wave disturbance or EL Nino was responsible for the creation of this assemblage as those events coincided.

Outer mainland shelf and upper slopes.—Sites on the outer mainland shelf and adjacent upper slopes (45–315 m) were inhabited by species from both the normal mainland shelf and mid-slope assemblages. Thus, the outer shelf-upper slope assemblage is transitional between the more distinctive mainland shelf and mid-slope assemblages (Table 2). Many sites in the outer shelf-upper slope assemblage were sampled repeatedly over time and due to variations in species composition and abundances, samples from one time would be classified with the normal mainland shelf assemblage and samples from another time would be classified with the outer shelf-upper slope assemblage. Many of the normal mainland shelf sites were classified as outer shelf-upper slope sites in 1982–1983, apparently due to the influx of *S. ingentis* and the tuna crab *Pleuroncodes planipes* during El Nino.

The most common and abundant species in the outer shelf-upper slope assemblage was *S. ingentis*. They were most abundant at the shelf-slope break (~150 m), but were collected at depths between 18–300 m. Abundances of this species varied by orders of magnitude over depth and time (Fig. 3). Abundances at the 100–200 m sites were highest in 1984, following El Nino, while abundances at sites shallower than 50 m remained rather constant. Abundances began to decline in 1985, and subsequent trawling in Santa Monica Bay (100–200 m) has shown a continuing decrease in its abundances through 1989 when abundances averaged less than 80 trawl⁻¹ (Thompson et al. 1991).

Another species that was very abundant in the outer shelf-upper slope assemblage was the tuna crab *Pleuroncodes planipes*. Although considered pelagic, they often rest on the sea floor. Its depth range in this study was 23–315 m, although a single specimen was collected on the Santa Monica Basin floor at 915 m.

Average abundances of *P. planipes* were very high because large numbers of adults of this species apparently immigrated into the region with El Nino (Table 2). They were rarely collected in trawl samples prior to 1983 (Fig. 3). In 1984, extremely large numbers (up to 44,220 trawl⁻¹) were collected at the 100–200 m sites, then abundances began to decline in 1985.

Mid-slopes.—Megabenthos on the slopes (300–490 m) of the San Pedro and Santa Monica Basins were quite different from assemblages at shallower and deeper sites. The mid-slope sites were dominated (abundance and biomass) by 3 species of echinoids: the regular echinoid *Allocentrotus fragilis*, and the irregular echinoids *Brissopsis pacifica*, and *Brisaster latifrons*.

The distribution and abundances of each echinoid were different over slope depth and on each basin slope (Thompson et al. 1987a). *A. fragilis* is an omnivore that lives on the sediment surface. They were collected between 100–480 m, with maximum densities at 300–400 m. *B. latifrons* is a burrowing deposit feeder that occurs between 200–600 m, with maximum densities near 400 m. They were much more abundant on the Santa Monica slopes than on the San Pedro slopes. *B. pacifica* is also a burrowing deposit feeder with maximum densities near 500

m, but they may range to sill depths, beyond the depth range of the other echinoids. In contrast with *B. latifrons*, they were more abundant on the San Pedro slope than on the Santa Monica slope.

The two irregular echinoids may occur in large scale herds (kilometers) on the slopes (Thompson et al. 1987a). Their burrowing creates a considerable amount of surface disturbance in slope sediments, but the effects of this activity on other slope benthos is unstudied.

Lower slopes.—The lower basin slopes assemblage inhabited sites between 478–780 m including a site on Redondo Knoll between the San Pedro and Santa Monica Basins. This assemblage was dominated by echinoderms. *B. pacifica* was the most common and abundant species, but ophiuroids and asteroids were also common and abundant (Table 2). Several species, the asteroid *Thrissacanthias penicillatus*, the gastropod *Bathybembix bairdii*, and the endemic demersal siphonophore *Dromalia alexanderii*, were collected only on the lower slopes.

There were differences in the abundances of some species between the San Pedro and Santa Monica Basin lower slopes. The epizoic ophiuroid *Asteronyx longifissus* was an order of magnitude more abundant on the Santa Monica Basin slope, but the asteroid *Myxoderma platyacanthum* was an order of magnitude more abundant in the San Pedro Basin slope. Factors that influence these differences are not known.

In 1982–1983, during El Nino, several species were collected on the lower slopes that were not collected in the 1977 or 1981 samples. These included the asteroids *Brisingella exilis*, *Ceremaster* sp., *Dipsacaster eximius*, and *Henricia polyacantha*, the pelecypod *Cyclopecten* sp., and the polychaete *Aphrodita japonica*.

Another feature of the lower slopes (and basins) was the sharp increase in the frequency of collection of sponges (Table 2). Hartman (1955) reported the occurrence of a “glass sponge zone” that ringed the lower slopes of the nearshore basins near sill depth. Several species of sponges were collected from these sites, but we have not identified them. These sponges provide a habitat for numerous ophiuroids, polychaetes, sipunculans, and fish. Factors that cause this increase in sponges near, and below the sills are not known.

Basin floors.—The sill depth of the San Pedro Basin is 737 m (Emery 1960) which corresponds closely to the separation of the lower slope and basin floor assemblages shown in the classification analysis. Eight trawls were collected below the sills in 1977 and 1985. One site located on the deepest part of Santa Monica Basin (915 m) was classified with the outer shelf-upper slope group because *P. planipes* was collected there. Another site (780 m) was inhabited by a diverse fauna, including echinoderms, and was classified as a lower slope site. Another site shallower than the sill (715 m) was inhabited by typical basin fauna, without echinoderms. These faunal variations around the sill demonstrate a variable lower slope-basin assemblage boundary in space and time.

The species composition of the megafauna in the basins is very different from the lower slope. Echinoderms were not collected on the basin floors. Instead, two species of galatheid crabs *Munidopsis hystrix* and *Munida quadrispina* were most abundant. Actually, the small gastropod *Mitrella permodesta* was most abundant in trawls, but it is a macrofaunal species (<4.2 cm, the trawl net size).

Below 850 m, Santa Monica Basin may be anoxic (Gorsline ms.) and has been considered biologically impoverished based on grab and core samples (Hartman

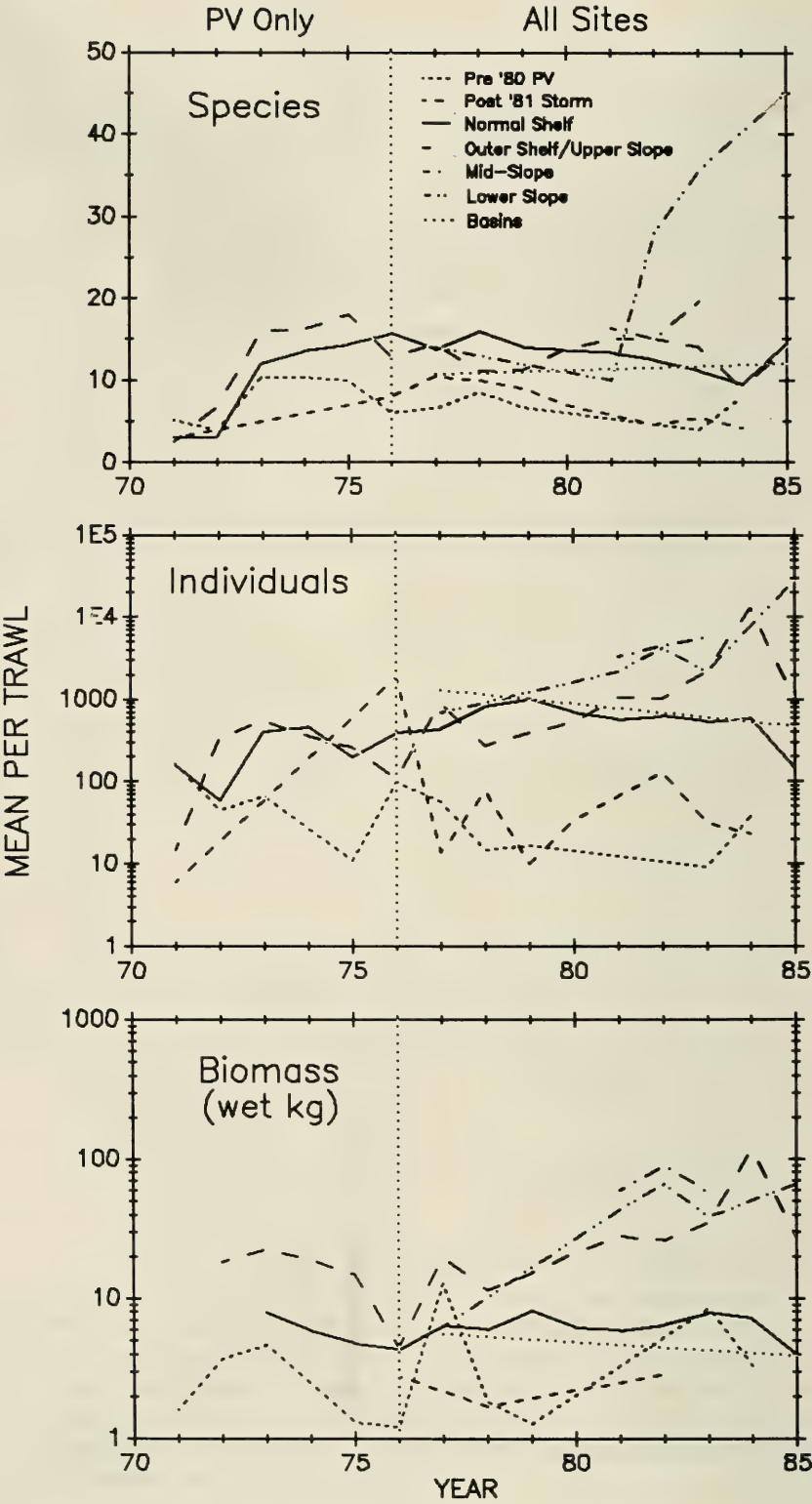


Table 3. Pooled mean (S.D.) number of species, individuals, and biomass per trawl in each megabenthic assemblage.

Megabenthic assemblage	No. trawls	Species	Individuals	Biomass (wet kg.)
Pre-1980 PV	78	5.8 (3.7)	68.3 (200.4)	3.0 (3.9)
Post-1981 storm/El Nino	29	5.6 (3.7)	101.0 (345.2)	0.9 (1.1)
Mainland shelf	658	13.1 (6.5)	577.0 (1539.0)	6.6 (11.3)
Outer shelf-upper slope	343	13.7 (6.0)	1869.5 (5347.4)	30.7 (53.5)
Mid-slope	25	18.0 (5.0)	4944.9 (4626.5)	64.2 (73.8)
Lower slope	17	29.5 (11.5)	3874.2 (6409.0)	48.6 (28.9)
Basins	6	11.0 (2.3)	1027.3 (1624.4)	3.9 (4.7)

1955, 1966; Fauchald and Jones 1979, 1983). However, all trawl samples from below the sills contained megabenthic organisms.

Trends in Numbers of Species, Individuals, and Biomass

The mean number of megafaunal species, individuals, and biomass per trawl increased over shelf and slope depths to maximum values in the mid- and lower slope assemblages (Table 3). Below the basin sills, these parameters decreased to values similar to those on the shelf. The large amounts of variation in these averages reflect both within-depth spatial heterogeneity (e.g., herds of urchins) and temporal variation.

Despite this variation, there were significant differences in some of these parameters between some of the classification assemblages. The pre-1980 PV and post-1981 storm/EL Nino sub-assemblages of the mainland shelf had significantly lower numbers of species and individuals than any other assemblage (Table 3; Duncan's multiple range test, $\alpha = 0.05$; Steel and Torrie 1960). Reduced abundances and biomass are typical of assemblages in contaminated areas (Pearson and Rosenberg 1978) and assemblages subjected to severe natural disturbances (Connell 1978). Although both anthropogenic and natural factors reduced numbers of species and individuals, megabenthic species composition (as measured by classification analysis) was somewhat different in response to each type of perturbation.

The mainland shelf and outer shelf-upper slope assemblages had similar numbers of species and individuals until 1982 when the number of individuals at the outer shelf sites increased considerably (Fig. 5). This increase was due to the influx of *S. ingentis* and *P. planipes* during El Nino. Biomass of the outer shelf-upper slope assemblage was consistently higher than on the mainland shelf due to the presence of large numbers of *S. ingentis*. Numbers of species, individuals, and biomass in the normal mainland shelf assemblage did not fluctuate significantly, even during El Nino.

The mid-slope assemblage had the highest number of individuals and biomass per trawl due to the large echinoid populations on the slopes as described above.

←

Fig. 5. Mean number of species, individuals, and biomass in each megabenthic assemblage per year. Vertical line at 1976 separates data from off Palos Verdes only and data from all areas of the region.

Table 4. Comparison of megabenthic assemblage depth ranges (meters) from 3 areas of the United States. Different assemblage designations (in parentheses) were used off Oregon.

Megabenthic assemblage	Southern New England ¹	Oregon ²	Southern California ³
		(Outer Sublittoral)	
Shelf	40–264	91–183	10–137
		(Upper Bathyal)	
Outer shelf-upper slope	283–650	185–457	45–315
		(Lower Bathyal)	
Mid-slope	653–1290	459–914	300–490
		(Bathyal-Abyssal)	
Lower slope	1380–1947	916–1554	478–780
Continental Rise	1947–3879	—	—
Basins	—	—	715–878
Abyssal	>3879	>1156	—

¹ Haedrich et al. 1980.

² Pereyra and Alton 1972.

³ This study.

Mid-slope samples were only collected in 1981–1983, thus long-term temporal changes were not observed.

The largest number of species per trawl occurred in the lower slope assemblage following El Nino. As detailed above, several species were collected on the lower slopes after 1982 that were not collected in the 1977 or 1981 samples. Additionally, abundances of many resident lower slope species increased during this time. The ophiuroids *A. longifissus* and *Ophiomusium jolliensis*, and the gastropod *B. bairdii*, all increased by an order of magnitude.

Numbers of species, individuals, and biomass decreased significantly below the basin sills (Duncan's multiple range test, $\alpha = 0.05$). Trawls were only collected from the Santa Monica and San Pedro Basin floors in 1977 and 1985, and the number of species, individuals and biomass were very similar in both the years sampled.

Discussion and Conclusions

Changes in soft substrata megabenthic assemblages off the southern California coast are primarily related to water depth. Major changes in species composition and abundances occur at mid-slope (~300 m) and at the basin sills (~737 m). Species composition of all assemblages appears to be seasonally stable as no separate winter or summer site groupings were identified in the classification analysis. However, on the mainland shelf megafaunal assemblages appear to have changed coincident with severe contamination, storms and/or El Nino.

There were no observable changes in overall species composition and abundances in any of the major megabenthic assemblages, except the mainland shelf, that appeared to be related to El Nino, e.g., there was no strictly El Nino site grouping in the classification analysis. However, abundances of several dominant species changed during, or following El Nino: *A. verrilli* increased during El Nino, *P. planipes* and *S. ingentis* increased by orders-of-magnitude following El Nino, but *L. pictus* decreased following El Nino. The most unexpected finding was the increased numbers of species and individuals (thus diversity) on the lower slope

following El Nino. The sharp increase in these parameters through 1985 suggests time delays in benthic effects from El Nino, but the processes involved are not known. There were no observable effects of El Nino on the basin assemblages.

The most dramatic change in megafaunal assemblages occurred near the basin sills. However, plots of sediment grain-size, organic material, and dissolved oxygen over slope and basin depths do not show any discontinuities at the sills that correspond with this major faunal break (e.g., Minard 1968; Gorsline ms.). The faunal break at the sills could be the result of episodic anoxia and flushing in the nearshore basins. Such episodes have been reported in the Santa Barbara Basin where anoxic bottom water was rapidly (weeks) flushed with water of higher oxygen concentrations, then decreased (months) back to anoxia (Sholkovitz and Gieskes 1971). Similar episodes may occur in the Santa Monica Basin (Gorsline ms.). Although episodic flushing may raise the dissolved oxygen concentration of basin water for an unknown period of time, that period of time may be insufficient for repopulation of the sub-sill basins before oxygen again decreases below megabenthic tolerances.

The presence of living megafaunal animals in the nearshore basins has not been previously reported. The sub-sill slope and floors of San Pedro and Santa Monica Basins are inhabited by up to 34 megabenthic species, but how they can exist in such low oxygen habitats is poorly understood. Current sediment biofacies models consider anoxic areas to be uninhabited by benthos (Savrdá et al. 1984; J. Thompson et al. 1985). Although few basin megabenthic species are deep burrowers and their activities may not produce bioturbation, their existence should be accounted for in models of animal-sediment interactions.

The numbers of megabenthic species, individuals, and biomass per trawl increased over shelf and slope depths, opposite to decreasing trends in those parameters for the macrobenthos (Thompson and Jones 1987). Maximum numbers of megafaunal species, individuals, and biomass occurred on the lower slopes. Factors that produce these maxima are not clear, but they reflect elevated levels of organic material. Although levels of organic material are even higher in the basins (6%, Gorsline ms.), dissolved oxygen concentrations may limit the kinds and abundances of megafauna there.

Previous collections of shelf megabenthos in Santa Monica Bay (Carlisle 1968) produced similar species composition as presented in this paper. Megabenthos collected from the Channel Is. shelves and offshore banks also included many species that inhabit the mainland shelf. *Allocentrotus fragilis* and the shrimp *Pandalus jordani* were the most abundant species in trawl samples (Mearns et al. 1978a). Insular species, such as the decapods *Clythrocerus planus* and *Crangon zorca*, occur along the mainland only in areas with coarser substrata (Wicksten 1980). At basin depths, megabenthos from the San Diego Trough, Santa Barbara Basin, and the offshore basins are quite different from those reported in this paper. The Santa Barbara Basin is anoxic which excludes most megafauna (Emery and Hulsemann 1962). The San Diego Trough is dominated by ophiuroids which do not occur in the northern nearshore basins (Barham et al. 1967). The San Diego Trough has no sill, thus the bottom water contains more dissolved oxygen (0.7 ml l^{-1} , Smith 1974) than in the northern nearshore basins. In the offshore basins, ophiuroids and holothuroids are dominant (Fauchald and Jones 1979; Smith and Hamilton 1983). These basins are deeper ($> 1000 \text{ m}$) but also have slightly higher

dissolved oxygen concentrations ($0.4\text{--}1.3\text{ ml l}^{-1}$, Emery 1960) than in the enclosed nearshore basins.

Factors that may control megabenthic assemblage zonation over depth encompass a wide variety of possible causes including trophic interactions, dissolved oxygen concentrations, and biological disturbance (Grassle et al. 1975; Haedrich et al. 1975; Rex 1981; J. Thompson et al. 1985). However, off southern California, factors that may be important, particularly biological interactions, remain unstudied.

The megabenthic assemblages identified off the southern California coast inhabit similar shelf and slope topography as those reported from other areas of the U.S. (Table 4). The major exception is the presence of several continental rise assemblages at the base of the slope off southern New England (Haedrich et al. 1980). No rise exists along the Pacific coast. Off Oregon, the megabenthos are similar to that reported in this paper. Echinoderms dominate the assemblages and biomass is highest on slopes (Pereyra and Alton 1972). The depth ranges of the megabenthic assemblages off the southern California coast are much narrower and appear much more compressed than those in other areas of the U.S. The difference is probably due to the shorter slope length and lower dissolved oxygen concentrations in the nearshore basins off southern California, but this situation has not been specifically studied.

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Gastrointestinal Helminths of the Western Brush Lizard, *Urosaurus graciosus graciosus* (Phrynosomatidae)

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Abstract.—Forty-one *Urosaurus graciosus graciosus* Hallowell, 1854, from Nevada and California were examined for helminths. Two lizards (5% prevalence) were infected with helminths. One female harbored one *Oochoristica* sp. and another female harbored one third stage *Physaloptera* sp. *Physaloptera* sp. is a new host record and is the first nematode recorded from *Urosaurus graciosus*. Helminth fauna of *U. graciosus* is compared to that of 22 lizard species from Riverside County, California.

The brush lizard, *Urosaurus graciosus* Hallowell, 1854, is a desert species which ranges from southern Nevada and western Arizona to northwest Sonora and northeast Baja California where it inhabits areas of loose sand and scattered brush, especially creosote bushes (Stebbins 1985). Two subspecies are recognized: the western brush lizard, *Urosaurus graciosus graciosus* Hallowell, 1854, and Arizona brush lizard, *Urosaurus graciosus shannoni* Lowe, 1955. To our knowledge there is but one previous report of helminths from *Urosaurus graciosus*. Telford (1970) reported a prevalence of 6% for the cestode, *Oochoristica scelopori* Voge and Fox, 1950. The purpose of this paper is to report the helminths of *Urosaurus graciosus graciosus* and compare them to helminth faunas found in 22 species of sympatric lizards.

Methods

Forty-one adult (29 female, 12 male) *U. graciosus graciosus*, mean snout-vent length (SVL) = 48.6 mm $\pm$ 4.0 S.D. (range 38–55 mm), were examined. Twenty were collected at Boulder City (35°59'N, 114°50'W) 747 m elevation, Clark County, Nevada during August 1935. Fifteen were collected at Palm Springs (33°49'N, 116°32'W) 142 m elevation, Riverside County, California in May 1970; three at Cadiz Lake (34°17'N, 115°23'W), 50 m elevation, San Bernadino, California in July 1972; one at Blythe (33°32'N, 114°35'W) 82 m elevation, San Bernadino County, California in April 1973, and two at Thousand Palms (33°49'N, 116°23'W) 61 m elevation, Riverside County, California in March 1971 (for Accession numbers see Appendix 1).

The specimens had been preserved in 10% formalin and were later stored in 70% ethyl alcohol. The body cavity was opened by a longitudinal incision from vent to throat. Gastrointestinal tract, liver, and body cavity were examined for helminths. Each helminth was identified using a glycerol wet mount. The cestode was stained with Delafield's hematoxylin utilizing the standard regressive staining technique and mounted in Canada balsam for study as a whole mount.

Table 1. Helminths of lizards from Riverside County, California.

Lizard family and species	Helminth	Prevalence	Reference
Anguidae			
<i>Elgaria multicarinata webbii</i>	<i>Physaloptera retusa</i> <i>Baerietta gerrhonoti</i> <i>Mesocostoides</i> sp.	13% (4/30) 63% (19/30) 7% (2/30)	Telford 1970 Telford 1970 Telford 1970
Crotaphytidae			
<i>Gambelia wislizenii</i>	<i>Atractis penneri</i> <i>Physaloptera retusa</i> <i>Thubunaea iguanae</i> <i>Oochoristica scelopori</i>	75% (3/4) 40% (2/5) 20% (1/5) 40% (2/5)	Telford 1970 Telford 1970 Telford 1970 Telford 1970
Gekkonidae			
<i>Coleonyx variegatus</i>	<i>Spauligodon californiensis</i> <i>Thubunaea iguanae</i>	56% (10/18) 11% (2/18)	Telford 1970 Telford 1970
Phrynosomatidae			
<i>Callisaurus draconoides</i>	<i>Atractis penneri</i> <i>Physaloptera retusa</i> <i>Spauligodon giganticus</i> <i>Thubunaea iguanae</i> <i>Mesocostoides</i> sp. <i>Alaeuris yumanae yumanae</i> <i>Atractis scelopori</i>	33% (2/6) 26% (5/19) 21% (4/19) 5% (1/19) 5% (1/19) 100% (1/1) 90% (19/21) 27% (4/15) 95% (20/21) 100% (2/2)	Gambino and Heyneman 1960 Telford 1970 Telford 1970 Telford 1970 Telford 1970 Telford 1970 Telford 1970 Gambino and Heyneman 1960 Telford 1970 Telford 1970
<i>Dipsosaurus dorsalis dorsalis</i>	<i>Atractis penneri</i> <i>Skrjabinoptera phrynosoma</i> <i>Atractis penneri</i> <i>Skrjabinoptera phrynosoma</i> <i>Atractis penneri</i> <i>Skrjabinoptera phrynosoma</i>	33% (1/3) 20% (1/5) 100% (2/2) 100% (1/1) 67% (2/3)	Gambino and Heyneman 1960 Telford 1970 Telford 1970 Telford 1970 Telford 1970 Telford 1970
<i>Phrynosoma coronatum blainvillii</i>			
<i>P. mcallii</i>			
<i>P. platyrhinos calidiarum</i>			

Table 1. Continued.

Lizard family and species	Helminth	Prevalence	Reference
<i>Sauromalus obesus obesus</i>	<i>Alaeuris priapus</i>	25% (3/12)	Telford 1970
	<i>Alaeuris sauromali</i>	100% (12/12)	Telford 1970
	<i>Alaeuris yumanae brevispicula</i>	17% (2/12)	Telford 1970
	<i>Atractis scelopori</i>	50% (1/2)	Gambino and Heyneman 1960
<i>Sceloporus graciosus vandenburgianus</i>		100% (12/12)	Telford 1970
	<i>Macdonaldius</i> sp.	8% (1/12)	Telford 1970
	<i>Spauligodon giganticus</i>	34% (24/71)	Telford 1970
	<i>Mesocestoides</i> sp.	1% (1/71)	Telford 1970
<i>S. magister magister</i>	<i>Ochoeristica scelopori</i>	10% (7/71)	Telford 1970
	<i>Atractis penneri</i>	50% (26/52)	Telford 1970
	<i>Thubunaea iguanae</i>	23% (12/52)	Telford 1970
	<i>Atractis penneri</i>	6% (7/116)	Telford 1970
<i>S. occidentalis biseriatus</i>	<i>Parapharyngodon iguanae</i>	1% (1/116)	Telford 1970
	<i>Physaloptera retusa</i>	13% (15/116)	Telford 1970
	<i>Spauligodon giganticus</i>	21% (24/116)	Telford 1970
	<i>Mesocestoides</i> sp.	1% (1/116)	Telford 1970
<i>S. orcutti orcutti</i>	<i>Ochoeristica scelopori</i>	23% (27/116)	Telford 1970
	<i>Atractis penneri</i>	17% (4/23)	Telford 1970
	<i>Parapharyngodon iguanae</i>	13% (3/23)	Telford 1970
	<i>Physaloptera retusa</i>	48% (11/23)	Telford 1970
<i>Petrosaurus mearnsi</i>	<i>Spauligodon giganticus</i>	13% (3/23)	Telford 1970
		4% (3/74)	Goldberg and Bursey 1991b
	<i>Thubunaea iguanae</i>	13% (3/23)	Telford 1970
	<i>Ochoeristica scelopori</i>	22% (16/74)	Goldberg and Bursey 1991b
<i>Uma notata</i>	<i>Parapharyngodon iguanae</i>	8% (2/24)	Telford 1970
	<i>Spauligodon mearnsi</i>	(?/2)	Egerly 1952
	<i>Strongyluris riversidensis</i>	63% (15/24)	Telford 1970
		(?/2)	Egerly 1952
<i>Uma notata</i>	<i>Atractis penneri</i>	50% (12/24)	Telford 1970
	<i>Skrjabinoptera phrynosoma</i>	27% (4/15)	Telford 1970
		53% (8/15)	Telford 1970

Table 1. Continued.

Lizard family and species	Helminth	Prevalence	Reference
<i>Urosaurus</i> <i>graciosus</i> <i>graciosus</i>	<i>Mesocostoides</i> sp.	20% (2/10)	Mankau and Widmer 1977
	<i>Oochoristica</i> <i>scelopori</i>	7% (1/15)	Telford 1970
	<i>Atractis</i> <i>pennieri</i>	100% (2/2)	Gambino and Heyneman 1960
	<i>Physaloptera</i> sp.	2% (1/41)	This study
	<i>Oochoristica</i> <i>scelopori</i>	6% (2/34)	Telford 1970
<i>Uta</i> <i>stansburiana</i> <i>stefmegeri</i>	<i>Oochoristica</i> sp.	2% (1/41)	This study
	<i>Atractis</i> <i>pennieri</i>	8% (51/639)	Telford 1970
	<i>Parapharyngodon</i> <i>iguanae</i>	1% (6/639)	Telford 1970
	<i>Physaloptera</i> <i>retusa</i>	3% (19/639)	Telford 1970
	<i>Thubunaea</i> <i>iguanae</i>	6% (38/639)	Telford 1970
	<i>Mesocostoides</i> sp.	14% (89/639)	Telford 1970
		5% (1/19)	Mankau and Widmer 1977
Scincidae			
<i>Eumeces</i> <i>gilberti</i> <i>rubricaudatus</i> <i>Eumeces</i> <i>skiltonianus</i>	<i>Acanthocephala</i> larva	17% (1/6)	Telford 1970
	<i>Physaloptera</i> <i>retusa</i>	7% (1/14)	Telford 1970
	<i>Mesocostoides</i> sp.	7% (1/14)	Telford 1970
Teiidae			
<i>Cnemidophorus</i> <i>tigris</i> <i>tigris</i>	<i>Pharyngodon</i> <i>cnemidophori</i>	31% (15/49)	Telford 1970
	<i>Skrjabinoptera</i> <i>phrynosoma</i>	2% (1/49)	Telford 1970
	<i>Thubunaea</i> <i>iguanae</i>	10% (5/49)	Telford 1970
	<i>Oochoristica</i> <i>bivittellobata</i>	27% (13/49)	Telford 1970
Xantusiidae			
<i>Xantusia</i> <i>henshawi</i>	<i>Thubunaea</i> <i>iguanae</i>	4% (2/51)	Telford 1970
	<i>Parapharyngodon</i> <i>californiensis</i>	40% (17/43)	Amrein 1951
		12% (6/51)	Telford 1970
<i>X. vigilis</i> <i>vigilis</i>	<i>Oochoristica</i> <i>scelopori</i>	21% (9/43)	Amrein 1951
		22% (11/51)	Telford 1970
	<i>Parapharyngodon</i> <i>californiensis</i>	22% (4/18)	Telford 1970
	<i>Oochoristica</i> <i>scelopori</i>	6% (1/18)	Telford 1970

Table 2. Amphibians and reptiles harboring third stage larvae of *Physaloptera* sp. (adults absent).

Host	Locality	Prevalence	Reference
Amphibia			
<i>Ambystoma opacum</i>	North Carolina	5% (1/21)	Mann 1932
<i>Desmognathus fuscus</i>	North Carolina	10% (4/41)	Mann 1932
	North Carolina	not given	Walton 1935
	North Carolina	2% (3/147)	Rankin 1937
	Georgia	not given	Reiber et al. 1940
<i>Plethodon glutinosus</i>	North Carolina	10% (4/39)	Mann 1932
	North Carolina	not given	Walton 1935
	Georgia	not given	Reiber et al. 1940
<i>Pseudotriton montanus</i>	North Carolina	33% (1/3)	Rankin 1937
<i>Acris crepitans</i>	Oklahoma	not given	Morgan 1941
	Ohio	10% (3/30)	Ashton and Rabalais 1978
<i>Hyla arenicolor</i>	Utah	41% (14/34)	Parry and Grundmann 1965
<i>H. versicolor</i>	Virginia	11% (3/28)	Campbell 1968
<i>Pseudacris brimleyi</i>	North Carolina	4% (2/55)	Brandt 1936
<i>P. crucifer</i>	North Carolina	3% (2/60)	Brandt 1936
	Oklahoma	not given	Morgan 1941
<i>Rana catesbeiana</i>	Oklahoma	not given	Morgan 1941
	North Carolina	20% (14/71)	Brandt 1936
	Ohio	8% (2/24)	Ashton and Rabalais 1978
	Virginia	7% (2/30)	Campbell 1968
<i>R. clamitans</i>	Virginia	17% (5/29)	Campbell 1968
<i>R. pipiens</i>	Utah	17% (5/29)	Parry and Grundmann 1965
	Wisconsin	not given	Morgan 1941
	Oklahoma	not given	Morgan 1941
	Ohio	33% (2/6)	Ashton and Rabalais 1978
<i>R. utricularia</i>	Oklahoma	not given	Morgan 1941
<i>Bufo alvarius</i>	Arizona	38% (36/95)	Goldberg and Bursey 1991a
<i>B. americanus</i>	Ohio	6% (2/34)	Ashton and Rabalais 1978
<i>B. cognatus</i>	Arizona	14% (3/21)	Goldberg and Bursey 1991a
	Oklahoma	not given	Morgan 1941
<i>B. speciosus</i>	Oklahoma	not given	Morgan 1941

Table 2. Continued.

Host	Locality	Prevalence	Reference
<i>B. houstonensis</i>	Texas	6% (1/17)	Thomas et al. 1984
<i>B. microscaphus</i>	Utah	13% (5/38)	Parry and Grundmann 1965
<i>B. woodhousii</i>	Utah	17% (1/6)	Parry and Grundmann 1965
	Oklahoma	not given	Morgan 1941
<i>B. woodhousii fowleri</i>	North Carolina	2% (1/61)	Brandt 1936
	Virginia	28% (8/29)	Campbell 1968
<i>Scaphiopus holbrookii</i>	North Carolina	3% (2/60)	Brandt 1936
Reptilia			
<i>Cnemidophorus dixonii</i>	Texas	19% (11/58)	McAllister et al. 1991
<i>C. exsanguis</i>	New Mexico, Texas	38% (9/24)	McAllister 1990c
<i>C. gularis</i>	New Mexico, Oklahoma, Texas	10% (29/289)	McAllister 1990d
<i>C. inornatus arizonae</i>	Arizona	1% (1/78)	Goldberg and Bursley 1990a
<i>C. laredoensis</i>	Texas	3% (1/34)	McAllister et al. 1986
<i>C. neomexicanus</i>	New Mexico, Texas	3% (2/61)	McAllister 1990b
<i>C. sexlineatus</i>	South Dakota	30% (7/23)	Dyer 1971
<i>C. tessellatus</i>	Texas	19% (5/27)	McAllister 1990a
<i>C. tigris</i>	Nevada	1% (1/97)	Babero and Mathias 1967
<i>Elgaria multicarinata webbi</i>	California	1% (1/96)	Goldberg and Bursley 1990b
<i>Heloderma horridum</i>	not given	not given	Morgan 1941
<i>Holbrookia maculata</i>	Arizona	7% (1/15)	Goldberg and Bursley 1992b
<i>approximans</i>	Arizona	3% (1/38)	Goldberg and Bursley 1992a
<i>Sceloporus scalaris slevini</i>	California, Nevada	2% (1/41)	this study
<i>Urosaurus graciosus graciosus</i>	Arizona, New Mexico	4% (8/205)	Goldberg et al. 1993
<i>U. ornatus</i>			

Results

One cestode, *Oochoristica* sp. was removed from the small intestine of a single female lizard, SVL = 47 mm (LACM 139654) and one nematode, a third stage *Physaloptera* sp. was recovered from the stomach of another female lizard, SVL = 50 mm (LACM 139661). Both helminths were recovered from the California subsample (Palm Springs and Cadiz Dry Lake). *Physaloptera* sp. represents a new host record for *U. graciosus graciosus*. Both helminths were deposited in the USNM Helminthological Collection, USDA, Beltsville, Maryland 20705: *Oochoristica* sp. (82303); *Physaloptera* sp. (82302).

Discussion

Telford's (1970) report of *Oochoristica scelopori* from 2 of 34 (6%) along with the 41 specimens we examined gives a combined total of 75 specimens and a helminth prevalence of 5%. These data suggest a depauperate helminth fauna for *U. graciosus* both in number of helminth species and in intensity of infection.

Of the sixteen species of nematodes, four species of cestodes and one species of acanthocephalan recovered from Riverside County, California lizards (Table 1), only one species of nematode and one species of cestode are known from *U. graciosus graciosus*. The lack of shared helminth faunas with sympatric lizards may be due to habitat and resource partitioning. According to Pianka (1973), lizards may partition three major resources: habitat, food, and time. *Urosaurus graciosus graciosus* is primarily arboreal and forages in the open canopy of small desert trees for arboreal insects (Vitt et al. 1981). The other lizards are ground dwellers (Stebbins 1985). Arboreal and ground-dwelling lizards feed on different prey which may help explain differences in parasite loads. Also, arboreal lizards may be able to avoid contaminated soil better than ground-dwellers.

The life cycles of species of both *Oochoristica* and *Physaloptera* have not been well studied. To date, all studies of *Oochoristica* life cycles (Millemann and Read 1953; Hickman 1963; Widmer and Olsen 1967; Conn 1985) and *Physaloptera* life cycles (Hobmaier 1941; Petri 1950; Petri and Ameel 1950; Schell 1952; Lincoln and Anderson 1975) indicate an insect intermediate host.

Third stage *Physaloptera* sp., but not adults, have been recovered from a variety of amphibians and lizards (Table 2). It should be noted that adults of species of *Physaloptera* are unknown from the Amphibia. Since insects serve as intermediate hosts to *Physaloptera* spp. as well as *Oochoristica* spp., diet may be the primary factor producing differential infection rates. However, Table 2 suggests that other factors are also important as *Physaloptera* fails to reach adult stages in at least 36 species of herptiles. Prevalence is variable among these species (Table 2), perhaps related to the proportion of insects in the diets, and thus potential infection. However, sufficient infection by third stage larvae of *Physaloptera* has been documented (note especially *Cnemidophorus* spp., Table 2) to suggest that some internal mechanism, perhaps some aspect of the physiology of these amphibians and reptiles, prevents survival of *Physaloptera* to the adult stage. The absence of *Oochoristica* sp. in some lizards suggests that similar physiological factors are operating here also. Much work remains to be done before the life history requirements of *Oochoristica* and *Physaloptera* are understood and why some herptiles serve as hosts while others present an unfavorable environment for parasites.

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Appendix 1

Boulder City, Clark County, Nevada (LACM, Natural History Museum of Los Angeles County, LACM 19022, 19030, 19043, 19044, 19046, 19048, 19055, 19061, 19063–19065, 19067, 19072, 19074, 19075, 19079, 19080–19082, 19085); Thousand Palms, Riverside County, California (LACM 139658, 139659); Palm Springs, Riverside County, California (LACM 139643–139657); Cadiz Dry Lake, San Bernadino County, California (LACM 139660–139662); Blythe, San Bernadino County, California (LACM 139663).

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